FEEDING ECOLOGY OF THE NEW ZEALAND CANCER CRAB *CANCER NOVAEZELANDIAE* (Jacquinot, 1853) (BRACHYURA : CANCRIDAE)

A thesis submitted in
partial fulfilment of
the requirements for the
Degree of
Master of Science in Zoology
at the
University of Canterbury

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University of Canterbury 1988

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ABSTRACT

This study investigates the predatory behaviour of Cancer novaezelandiae (Decapoda : Brachyura : Cancridae), a subtidal crab from Lyttelton Harbour, Banks Peninsula.

Cancer crabs were obtained at bimonthly intervals over a 22 month sampling period. Examination of stomach contents suggested that C.novaezelandiae was an opportunistic predator feeding on a wide variety of food items. Molluscs composed the major components of diet, with bivalves and gastropods comprising 35 % of all food items. Crustacea were the next most important group comprising 20 % of all food items. Amphipods, isopods and crabs were the most frequent crustaceans found. Other food types included fish, sponges, coelenterates and plant matter in relatively low abundances. No variation in dietary composition was evident with crab sex, size or season.

The functional morphology of the chelae, mouthparts and gastric mill were examined for two size-classes of crab (60.0-70.0 and 120.0-130.0 mm carapace width). The mouthparts and gastric mill were generalised in structure and were typical of large, predatory brachyurans. Large crista dentata of the third maxilliped and sharp, rounded mandibles, together with large, heavily chitinised gastric mill ossicles suggested that C.novaezelandiae was well equipped to macerate course, particulate matter. No variation in either mouthparts and gastric mill structure was evident with crab size or sex. Left and right

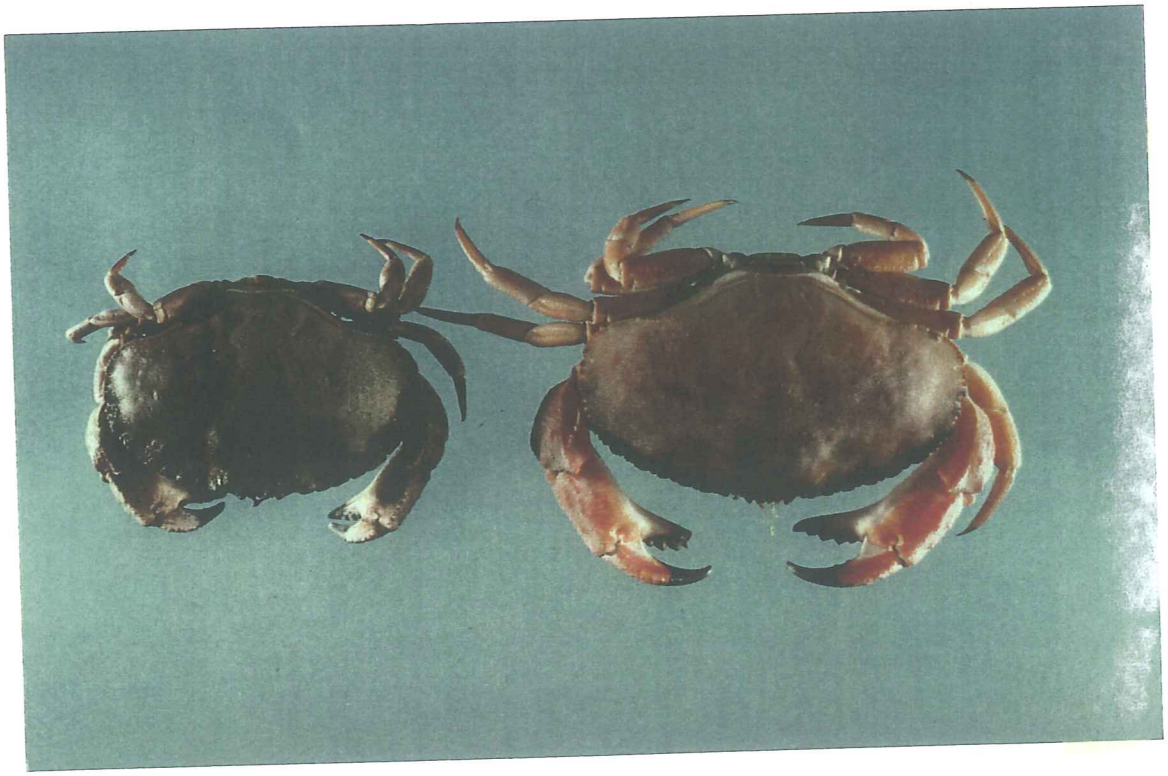
chela of C.novaezelandiae were morphologically similar in shape and dental pattern, and no difference was found between sexes. Relative growth of the chelae was described from measurements made on propodus height and length using carapace width as the reference dimension. Log-transformed regressions were used to test for allometric growth and lines were compared using t-tests. No significant difference was found in the growth of the propodus between left and right chelipeds, and for males and females. Relative growth of the propodus was positively allometric which remained constant throughout crab growth. No discontinuity in growth of the propodus was evident for male and female crabs (however, for male crabs over 110 mm carapace width there was a slight indication of increased propodus growth). Both left and right chela of male and female crabs had a large diastema, and mean mechanical advantage of 0.367 and 0.375 respectively. The high mechanical advantage of the chela in C.novaezelandiae appeared to remain constant throughout crab growth, allowing a compressive force in excess of 496 $kN.m^{-2}$. The polyfunctional chela are therefore, capable of holding, manipulating and crushing a variety of prey shapes.

Predator-prey experiments were undertaken in the laboratory using male crabs of three size classes (55.0-65.0, 80.0-90.0 and 105.0-115.0 mm carapace width). Prey used included blue mussel Mytilus edulis aoteanus, cockle Chione stutchburyi, spotted whelk Cominella maculosa and catseye Turbo smaragdus. C.novaezelandiae adopted five distinct techniques to open bivalve and three techniques to open gastropod shells. The particular opening

technique used was influenced by crab size, prey size and success of previous attempts. Small molluscs were usually opened by direct crushing by the chela and/or mouthparts. Splitting of the umbone valves and removal of the aperture lip were the most successful techniques used to open large bivalves and gastropods respectively. Handling times increased exponentially with prey size, with large crabs requiring less time to open prey than small crabs. Prey species influenced handling times with bivalves opened more quickly than gastropods. Critical maximum prey size increased with crab size, while minimum critical size was smaller for small crabs. Different sized crabs consumed similar numbers of prey, but energy intake increased with crab size. Profitability curves were derived and tested with regard to optimal prey size and species. When presented with a size range, crabs selected prey sizes that minimized time spent foraging. However, when presented with different prey species, crabs maximized energy intake by selecting optimum prey species. Findings suggested C.novaezelandiae exhibited a flexible foraging behaviour, which allows crabs to maximize feeding efficiency. This was discussed in the context of the ecology of the crab and the Energy Maximization Premise (Elner and Hughes, 1978).

Plate 1. Male *Cancer novaezelandiae*.

Plate 2. Dorsal view of male crabs;
110.5 mm carapace width (left),
85.7 mm carapace width (right).



CHAPTER ONE

GENERAL INTRODUCTION

The way in which predators select, catch, handle, ingest and digest their prey is crucial to the understanding of predator-prey systems, particularly with regard to identifying the factors regulating these interactions. Examining both structural and behavioural adaptations enabling both predator and prey to co-exist, facilitates a better understanding of how predator-prey interactions are maintained.

Within natural communities exists intimate relationships between members of the food chain, and as such, brachyuran crustaceans form an integral component within the food chains of coastal areas. Knowledge of coastal ecosystems requires detailed information on the precise nature of relationships within and between species.

It has long been recognized that crabs are important predators of molluscs, notably bivalves and gastropods (Menzel and Hopkins, 1956; Walne and Dean, 1972; Elner and Hughes, 1978; Whetstone and Eversole, 1978; Elner and Raffaelli, 1980; Wear, 1984; ap Rheinallt and Hughes, 1985; Wear and Haddon, 1987. Numerous investigations have examined how crabs locate, obtain, select, handle and consume prey. However, the majority of these studies pertain to a few brachyuran families, especially Portunidae. Also there is a tendency to use closely related prey

species for all studies, particularly the bivalve Mytilus edulis. This emphasis on a few predator and prey species may lead to over-simplication and wide generalizations regarding the mechanisms used in brachyuran feeding. Crabs show a wide diversification with respect to structural, behavioural and locomotory adaptations, therefore they may be expected to exhibit a variety of feeding strategies. Moreover, M.edulis may not be representative of all molluscs species. Therefore, in order to fully understand brachyuran-mollusc prey feeding relationships, a wider array of brachyuran families and mollusc types need to be examined.

Several studies have examined the feeding ecology of cancrid crabs. These include Cancer magister (Gotshall, 1977; Feder and Paul, 1980; Asson-Batres 1986), Cancer irroratus (Scarratt and Lowe, 1972), Cancer pagurus (Feare, 1970; Muntz, Ebling and Kitching, 1965, Lawton and Hughes, 1985). To date, little information is available regarding the feeding ecology of the New Zealand cancer crab Cancer novaezelandiae (Plate 1 & 2). This is limited to an analysis of the gut contents of a small number of crabs collected from the Avon-Heathcote Estuary (Thompson, 1930). There is no information describing how C.novaezelandiae obtains, handles, selects and consumes different prey species.

C.novaezelandiae is a relatively common species of harbours, estuaries and coastlines (Bennett, 1964). It is an endemic species found throughout New Zealand including the Auckland and Chatham Islands. It has been suggested that it has been self or

accidentally introduced to southern-eastern Australia and Tasmania (McLay, pers. comm). Male C.novaezelandiae grow to a maximum carapace width of 150 mm. It is a subtidal species found in a range of depths between 0 and 60 m (Bennett, 1964). The crab can be found buried in fine sediment, or under rocks, stones and amongst seaweeds along both hard and soft coastlines. Juveniles are found in shallow rocky areas usually living amongst seaweeds for protection. Breeding has been recorded in January and May, with females carrying up to 12,000 eggs (Bennett, 1964). Larvae are present in surface waters from September and October (Wear and Fielder, 1985).

The New Zealand cancer crab is closely related to both the edible European and American cancer crabs C.magister, C.pagurus and C.irroratus. These species form an important commercial resource; however, the potential for C.novaezelandiae to support a viable crab fishery in New Zealand has yet to be established. If C.novaezelandiae is to be exploited in the future, detailed knowledge of the crabs' feeding ecology is essential.

This study investigates the feeding ecology of C.novaezelandiae, and where possible, findings from both field and laboratory experiments have been integrated. Chapter One is an investigation into the natural diet of crabs from Lyttelton Harbour. The aim was to investigate dietary components and the influence of crab size, sex and season on diet. Findings enabled the determination of prey species to be used for laboratory investigations. A study of the functional morphology of the

feeding apparatus of C.novaezelandiae is described in Chapter Two. The aim was to examine the morphology of the chelae, mouthparts and gastric mill of different sized individuals, and to investigate chelae growth and mechanical properties with respect to crab size and sex. Chapter Three describes prey selection and profitability, opening techniques, handling times, consumption rates and critical prey size. These findings were placed within the framework of the Optimal Foraging Theory. The final chapter relates the findings of this thesis to the ecology of C.novaezelandiae in Lyttelton Harbour.

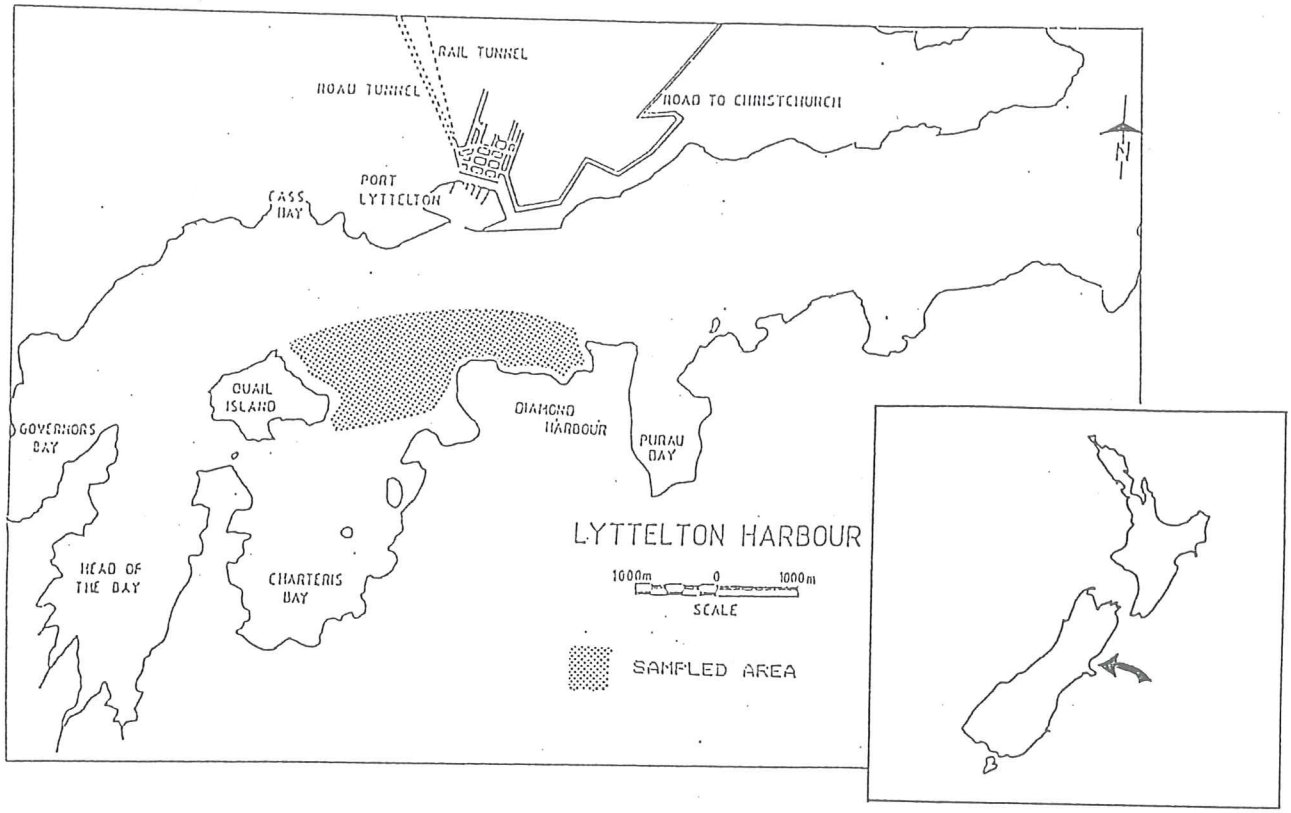
STUDY AREA

Lyttelton Harbour (43° 38'S, 172° 44'E) is typical of the shallow, muddy bottom inlets that indent the coastline of New Zealand. It is an extensive marine inlet with a axis running east-west, opening to the sea on the northwest side of Banks Peninsula (Figure 1.1, Plate 3). The harbour is 15 km long, approximately 1.6 km wide and encompasses an area of 44 km^2 (Knox, 1983).

Depth decreases from 16.5 m at the harbour entrance to shallow mudflats at the head. Over a large area surrounding Quail Island, Charteris Bay and Purau Bay depth is a constant 3.5-6.5

Figure 1.1. Map of Lyttelton Harbour. Sampling area is shown.

Plate 3. View of study area.


RAIL TUNNEL
ROAD TUNNEL
ROAD TO CHRISTCHURCH
N
PORT LYTTELTON
CASS BAY
QUAIL ISLAND
DIAMOND HARBOUR
PURAU BAY
GOVERNORS BAY
HEAD OF THE BAY
CHARTERIS BAY
LYTTELTON HARBOUR
1000m 0 1000m
SCALE
SAMPLED AREA

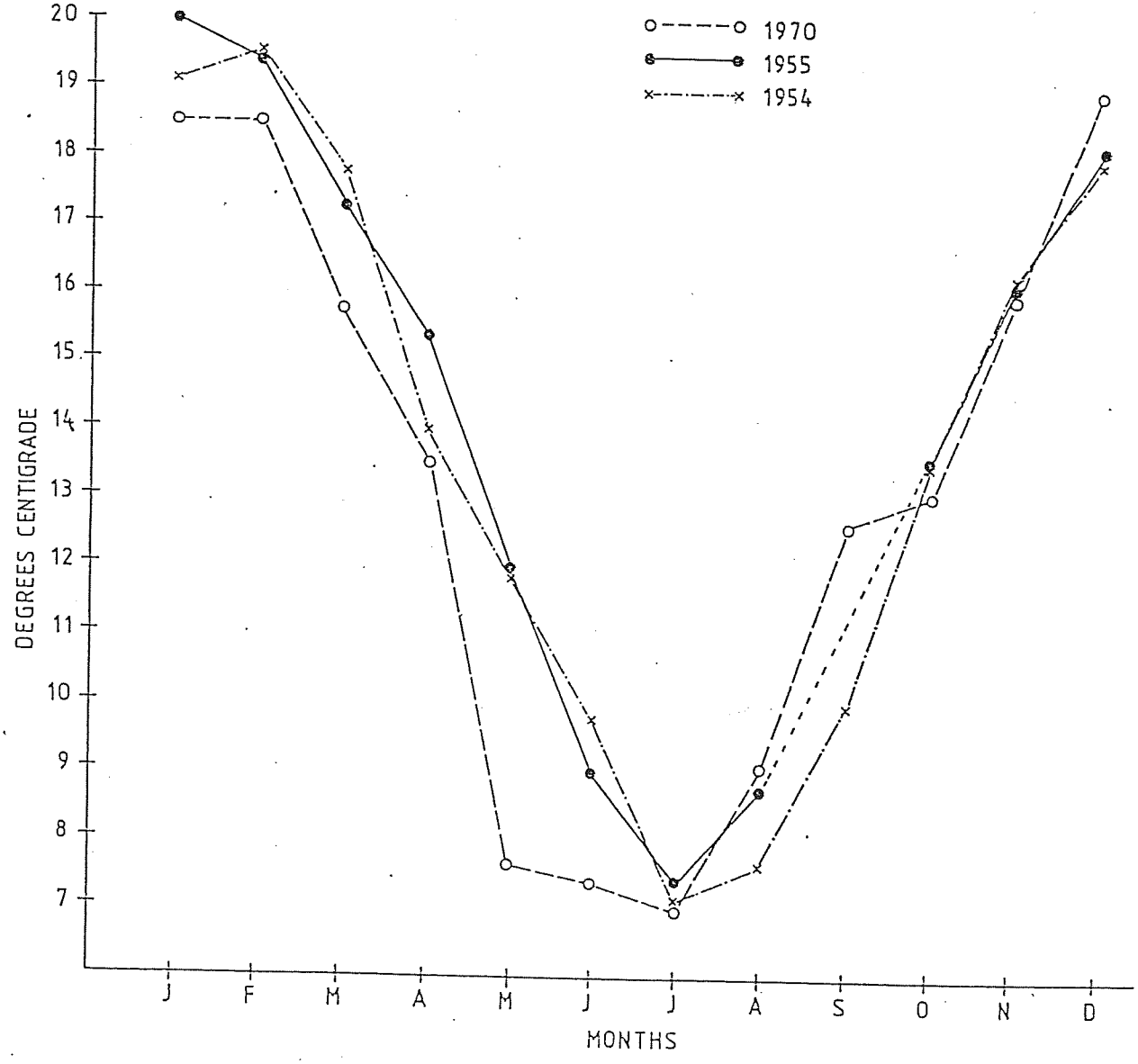
m. At low tide, a quarter of the total harbour area is exposed as mudflats against the developed upper reaches. The tidal range varies between 1.92 m (spring tide) and 1.64 (neap tide). Tidal circulation within the harbour is generally significant (Millhouse, 1977).

Wave action within the harbour is generally small, although disturbance of sediment in the upper harbour is frequent. There is a large annual variation in sea temperature ranging from 7-20^{o}C. This variation appears to remain constant year to year (Figure 1.2).

Water turbidity is particularly high within the harbour due to regular dredging of the harbour channel by the Lyttelton Harbour Board. As a result sediment load within the water column is high, leading to high silt deposition of the harbour substratum.

Most of the harbour shore is fringed by cliffs giving way to a small, steep rocky intertidal region. Within this region typical zonation patterns occur supporting large populations of typical rocky shore fauna. Dominant species within the intertidal region include molluscs Littorina unifasciata, Littorina cincta, Mytilus edulis aoteanus, limpets Patelloida corticata, Cellana radians, Notoacmea parviconoidea, barnacles Elminius modestus, Chamaesipho columna, and annelids Spirorbis spp., Pomatoceros cariniferus (Knox, 1983). Large beds of Macrocystis pyrifera are a predominant feature within the intertidal region. At a depth of

Figure 1.2. Annual ranges of temperatures in Lyttelton Harbour for the years 1954, 1955 and 1970 (Knight, 1971).


1970
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1.0-1.5 m the rocky intertidal region gives way to very soft mud and sand, extending outwards into the mid-channels of the harbour. This substratum is composed of a combination of fine silt, sand and bottom mud containing high organic content and is generally anoxic (Knight, 1971).

A limited number of scientific studies have been undertaken within Lyttelton Harbour. Knight (1971) and Knox (1983) extensively examined physical and biotic features in both intertidal and subtidal regions. Both authors agreed that a wide variety of benthic animals inhabit the substrata of both regions.

Within the intertidal region Knox (1983) recorded 109 species including 35 algal species and 74 animal species. Animal fauna included 27 molluscs (Mollusca), 14 arthropods (Arthropoda), 7 polychaetes (Polychaeta), 6 sponges (Porifera), 6 bryozoans (Bryozoa), 5 sea squirts (Ascideacea) 3 hydroids (hydrozoa), 2 sea anemones (Anthozoa), 2 starfish (Asteroidea). Amongst the molluscs, 5 chitons (Amphineura), 17 gastropods (Gastropoda) and 5 bivalves (Bivalvia). While amongst the arthropods there were 5 isopods (Isopoda) and 3 decapods (Decapoda). Highest abundance were found in the eulittoral zone with approximately 22,000 m^{-2} recorded.

Within the subtidal region extending outwards into the mid-channels of the harbour, a total of 16 species were recorded. Species included 1 nematode, 9 polychaetes, 2 crustaceans and 1

bivalve. Densities were considerably lower in the subtidal region with a mean of 1199 m^{-2}.

Knight (1971), however, found a considerably greater number of species inhabiting the benthos recording 119 animal species. These included 42 mollusc (18 bivalve and 19 gastropod species) and 24 arthropods (9 decapod species). Moreover, he found highest densities of animals correlated well to sandy-mud portions of the harbour. In particularly, to an area extending from Ripapa Island to Quail Island, where extensive beds of Chione stutchburyi predominate.

Species within the Lyttelton harbour have been shown to be patchily distributed (Knight, 1971). High water sediment load, tidal currents and anoxic substratum conditions have been suggested as principle factors restricting prey distribution. High densities of C.stutchburyi were found around the coasts of Quail Island and extend eastwards to Ripapa Island along the path of the flood tide. Cockle biomass of 10,000 grams m^{-2} have been recorded within these beds. Similar beds were found in mid-harbour but were less dense. Spat survival rate has been attributed to limited cockle distribution within the harbour. Gastropod Micrelenchus huttoni exists in both sandy and muddy substrata, but show highest densities when associated with algal mats in the upper harbour. Bivalves Nucula hartvigiana and Mariomactra ordinaria was restricted to areas around Quail Island and Charteris and Purau Bays respectively. Molluscs species Ostrea heffordi, Trochus tiaratus, Xymene plebejus, Sigapatella

novaezelandiae and Achelia variabilis have all been shown to be restricted within the benthos of Lyttelton Harbour (Knight, 1971).

Despite restrictions in prey distribution, both Knight (1971) and Knox (1983) concluded that Lyttelton Harbour has a high faunal diversity in both intertidal and subtidal habitats.

CHAPTER TWO

NATURAL DIET OF *CANCER NOVAEZELANDIAE*

INTRODUCTION

Many brachyurans are opportunistic predators of benthic macro-invertebrates, and as such, they form an important component of the benthic ecosystem. Natural diet has been investigated for numerous crab species, including Cancer irroratus (Scarratt & Lowe, 1972); Cancer magister (Gotshall, 1977; Feder & Paul, 1980; Stevens, Armstrong & Cusimano, 1982); Ovalipes catharus (Kung, 1973; Wear, 1984; Davidson, 1987; Wear & Haddon, 1987); Ovalipes stephensoni (Haefner Jr., 1985); Carcinus maenas (Ropes, 1968; Elner, 1981); Liocarcinus puber, Liocarcinus holsatus (Choy, 1986); Callinectes arcuatus, Callinectes toxotes (Paul, 1981); and Scylla serrata (Hill, 1976). Many of these studies were initiated in response to declining stocks of commercially important shellfish.

The studies mentioned above are largely based on small samples taken from a single habitat at a particular time, and which only describe the diversity of prey species eaten. There is little information on the effects of crab size, sex, season, or stage of the moult cycle on dietary trends. This lack of information is surprising as investigations of crab nutritional requirements, interactions with other animals and commercial

potential essentially require detailed quantitative knowledge of natural diet (Williams, 1981).

Cancer novaezelandiae is a common species in harbours, estuaries and along coasts throughout New Zealand. Despite its occurrence and commercial potential, previous accounts of diet in this species are sparse and mainly anecdotal. Thompson (1930) reported that C.novaezelandiae collected from the Avon-Heathcote Estuary, New Zealand were found to have pieces of shellfish and worms in stomachs. Cockles, oysters and flesh from open mussel shells were also found to be consumed (Bennett, 1964). It is commonly caught in traps baited with fish but it is not known whether fish forms a part of its natural diet. There is an increasing interest in the aquaculture of C.novaezelandiae, and in this field it would be important to know which types of food are eaten by the crab under natural conditions.

This study examines the natural diet of C.novaezelandiae from Lyttelton Harbour, Banks Peninsula. Dietary composition was determined from bimonthly fore-gut analyses of crabs collected from intertidal and subtidal areas. The aim was to determine variations in dietary composition due to crab size, sex and season. The information was also used to determine potential prey items for use in laboratory studies.

METHODS AND MATERIALS

Sample Collection

C.novaezelandiae were collected from Lyttelton Harbour between June 1985 and April 1987. Crabs were collected both intertidally and subtidally from an area between Quail Island and Diamond Harbour on a bimonthly sampling regime (Figure 1.1). Crabs were collected using two types of sampling techniques; trapping and trawling. Both techniques have been used in previous crab studies where they were successful in collecting male and female crabs of a wide size range (Steven, Armstrong & Cusimano, 1982; Jewett & Feder, 1982; Davidson, 1987; Wear & Haddon, 1987).

One metre square traps made of 10 mm wire mesh were baited with fresh scraps of fish (hoki Macruronus novaezelandiae, ling Genypterus blacodes, red cod Pseudophycis bacchus) enclosed in 0.1 mm nylon mesh bags and tied securely to the centre of the trap. Crabs were therefore attracted to the trap but were unable to obtain fish from it. Traps were lowered over the side of Diamond Harbour wharf to a range of depths from 1.0-4.5 m. Traps were left for a period of 15 minutes after which, they were hauled up and all crabs caught were removed. All collections were made 1-2 hours after sunset to coincide with approximate time of maximum feeding activity.

The second method of collection involved random 10 minute trawls using a 1.5 m beam trawl (10 mm mesh net and a 2 mm mesh cod-end). Trawls were taken between Quail Island and Diamond

Harbour at depths of 3.0-6.0 m. Collections were taken between 0900-1200 hours. The time of collection was considered most appropriate in order to maximize collecting crabs previously feeding during the last sunset-sunrise period. Both techniques were used to sample from as wide an area as possible, and thus obtain crabs from a range of substrata.

Fore-gut Analysis

All crabs used for gut analysis were killed immediately after capture. Crabs were killed by piercing the dorso-cardiac region and placed immediately into 10 % Formalin. The rapid process of preserving crabs was important as Hill (1976) suggested that decapods rapidly clear food from the fore-gut. In the laboratory, the sex of each crab was recorded, carapace width was measured (see Chapter Three) using Vernier calipers and the moult stage recorded. The gastric mill (proventriculus) was extracted and its contents were emptied into a petri dish and examined under a binocular microscope.

Diet was assessed in two ways, 1) percentage occurrence method and 2) points method, both of which evaluate abundance and volume. These methods have been commonly used to describe stomach contents in brachyurans (Paul, 1981; Williams, 1981; Almarzah, 1985; Choy, 1986; Wear & Haddon, 1987). The mastication of food by chelae, mouthparts and gastric mill make exact quantitative determination of abundance and volume difficult. Where possible food items were recorded to species level. In the analysis of results, food items were grouped into ten taxonomic categories

such as, bivalves and gastropods, amphipods and isopods, and crabs.

Frequency of occurrence of each food category was recorded for each crab on a presence or absence basis. The relative contribution of each food category to the overall abundance and volume of food content within the stomach was subjectively assessed using a points method. The amount of each food item in the fore-gut was estimated visually and allocated points depending upon gut fullness and the relative contribution of each food category. For example, a full stomach indicated by a distended fore-gut was allocated 100 points, and one-quarter full stomach was given 25 points. The relative amount of each food category was estimated and allocated points. Therefore a mass of bivalves making up three-quarters of the bulk of a full stomach is worth 75 points (0.75 x 100), while the remaining one-quarter comprising of crustacea is worth 25 points (0.25 x 100).

Statistical Analysis

Data from both points and frequency of occurrence methods were expressed in percentage terms based on total food items found in stomachs containing food, not on the total number of stomachs examined. Statistical analyses were performed on frequency of occurrence of ten food categories. Variations in diet with season and crab size were examined by combining data from both sexes. Effects of crab size and sex on diet were investigated using data obtained over the entire sampling period. Seasonal variation in diet was examined using 1986 data only.

The relationship between size and age of postmetamorphosis crabs is not known for C.novaezelandiae. Therefore size classes small (40.0-60.0 mm), medium (61.0-100.0 mm) and large (101.0-160.0 mm) carapace width were used in the present study to examine effects of crab size on diet.

The Spearman rank correlation test was used to test the correlation between frequency of occurrence and percent volume of fore-gut contents. Feeding differences between males and females, crab size classes and seasons were tested using Chi Square tests on frequency of occurrence data using a 5 % level of significance.

Fore-gut Analyses As A Method Of Diet Estimation.

Most previous studies of brachyuran feeding have used the same two techniques of dietary estimation employed for this study (Hill, 1976; Elner, 1981; Paul, 1981; Stevens, Armstrong & Cusimano, 1982; Williams, 1982; Choy, 1986; Wear & Haddon, 1987). Both techniques proved successful in quantifying dietary components. However, Williams (1981) suggests that the nature of each food type and the way in which it is manipulated by the chelae and mouthparts affect the accuracy of the percentage points estimates, and to a lesser extent, percent occurrence estimates of some food types. Since soft parts of most foods become rapidly unrecognizable after ingestion, the points method is inaccurate for most food types. However, it is suitable for foods which are ingested in large recognizable pieces.

The degree of relative importance of a particular food type is measured by percent occurrence. However, this method is only accurate for food with recognizable hard parts, such as shell and crustacean exoskeleton remains. Therefore soft-bodied food items such as coelenterates would be underestimated. However in the present study, because soft-bodied animals without skeletons were rarely encountered in gut remains, underestimation was considered negligible.

Despite shortcomings, both techniques proved successful in both quantitatively and qualitatively describing the diet. This is reflected by good correlations between the two methods.

RESULTS

From a total of 547 crabs collected between June 1985 and April 1987, 186 (34%) contained ingested material in the fore-gut. Although the remaining 361 (66%) of stomachs were devoid of any solid material, many of these were filled with a clear fluid. Crabs with food items in the stomach consisted of 120 (64.2%) males and 66 (35.8%) females, and ranged in size from 40.0 mm to 135.0 mm carapace width. Almost all (98.9%) of the crabs found with filled stomachs were collected in a hard-shell condition. Only one ovigerous female was collected and it was found to possess food items in the fore-gut.

Fore-gut Contents

The majority of food items within the gastric mill appeared crushed or finely fragmented. The extent of mastication varied with food types eaten, the degree of mouthpart and chelae manipulation and gastric mill grinding. Food typically consisted of small (< 3.0 mm.) hard fragments and large strands of macerated soft tissue. Remains of food items with hard parts were easily identified to generic or species level. However, soft-bodied animals were more difficult to identify and more generalized taxonomic categories had to be used. Within stomachs containing food, 15 species were found. Phyla represented included Mollusca (bivalves, gastropods and cephalopods), Crustacea (amphipods, isopods, brachyurans and shrimps), Porifera (sponges), Coelenterata (sea anemones and hydroids), Chordata

(fish) and Algae (brown, Phaeophyceae; green, Chlorophyceae and red algae, Rhodophyceae; Table 2.1).

Skeletal structures were used primary to identify prey in stomachs. Bivalves and gastropods were identified by shell fragments, tissue, periostracum chips and gill filaments. Cephalopods were identified by epidermal chromatophores. Crustaceans were identified by distinct chitinous plates, exoskeleton fragments, appendages including limbs, mouthparts, spines, eyestalks, antennae and fore-gut ossicles. Prey items including Porifera and Coelenterata were identified by reproductive bodies and distinct spicules. Muscle, scales, skeletal fragments, jaws, teeth and fin rays indicated fish material. Algae was identified by distinct groupings of cells and could be separated into brown, green and red algae. Identification of food items was not always possible due to its digestive condition, therefore this material was placed into a separate unidentified category. A large proportion of unidentified material appeared to be of mollusc origin without recognizable shell fragments or periostracum.

Effects Of Crab Sex, Size And Season On Diet.

A wide variety of food items were found from gut samples. However, diet was composed of two main categories : Mollusca and Crustacea. Bivalve and gastropod molluscs constituted the major dietary components both in terms of percentage occurrence and percentage points. Molluscs composed one-third of all food items found. Species positively identified included Mytilus edulis

Table 2.1. List of organisms and their identifying features removed from the fore-guts of *C.novaezelandiae* from Lyttelton Harbour between June 1985 and April 1987 (n=187).

FOOD TYPES	TYPES OF FRAGMENTS
MOLLUSC	
Bivalve / Gastropod *Mytilus edulis aoteanus* *Amphidesma australe* *Chione stutchburyi* *Venerupis largillieriti* *Paphies australis* *Cominella maculosa*	Shell fragments, tissue, gill filaments, periostracum chips.
Cephalopod *Octopus maorum*	Chromatophore covered flesh.
CRUSTACEA	
Amphipod / Isopod *Isocladus armatus*	Exoskeleton fragments : including appendages ie. limbs, thoracic plates, antenna, spines, eyestalks.
Crab / shrimp *Cancer novaezelandiae* *Nectocarcinus antarcticus* *Callianasa filholi* *Halicarcinus whitei* *Hemigrapsus edwardsii* *Upogebia hirtifrons*	Fragmented exoskeleton : including carapace and leg fragments. Gills, eyestalks, gastric mill ossicles, mouthparts (incl. maxillipeds, maxilae, and mandibles).
TELEOST Pleuronectidae	Muscle and fibres, scales, skeletal fragments, jaw, teeth, fin rays.
PORIFERA	Spicules, spores.
COELENTERATA Hydroids Sea anemone *Anthopleura aureoradiata*	Mass of tentacles, stalk.
PLANT Green Algae Brown Algae Red Algae	Small pieces of frond : groupings of cells.

aoteanus, Amphidesma australe, Chione stutchburyi, Venerupis largillierti, Paphies australis, and Cominella maculosa. Cephalopods formed only a small proportion of the diet.

Crustacea were the second most important food category composing one-fifth of the diet. They included isopods such as Isocladus armatus, crabs C.novaezelandiae, Nectocarcinus antarcticus, Halicarcinus whitei and Hemigrapsus edwardsi. The shrimps Callianassa filholi and Upogebia hirtifrons occurred infrequently.

Fish, sponges and coelenterates were infrequently encountered. Furthermore, algae was also rarely found, and occurred in only small quantities.

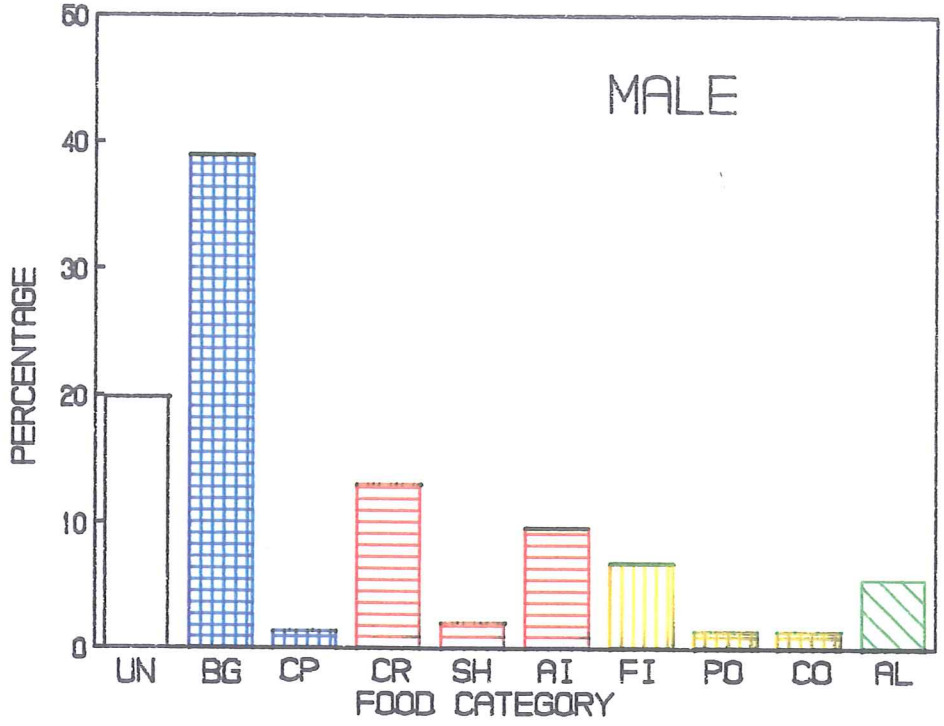
For both male and female crabs over the entire sampling period, a high correlation between the two methods of assessing diet was found (male r=0.89; female r=0.99, n=10). Therefore, because there was good correlation between the two methods of estimation of gut contents, frequency occurrence alone was subsequently used for statistical comparisons between sex, size and season.

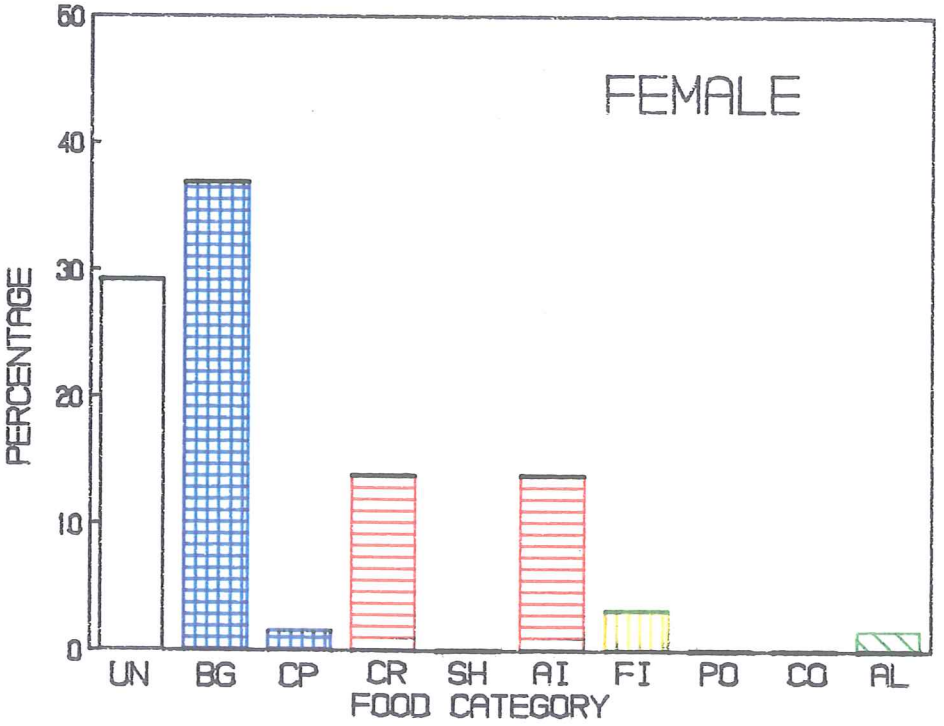
The dietary composition of male and female crabs was similar (X^2=8.447, df=9, NS, Fig. 2.1). Both males and females were found to have the same food types in relatively similar proportions.

Figure 2.1. Percentage frequency of occurrence for male (n=120) and female (n=67) crabs collected between June 1985 and April 1987.

KEY

UN = Unidentified material.
BG = Bivalves and gastropods.
CP = Cephalopods.
CR = Crabs.
SH = Shrimps.
AI = Amphipods and Isopods.
FI = Fish.
PO = Porifera.
CO = Coelenterates.
AL = Algae.


MALE
PERCENTAGE
0
10
20
30
40
50
UN
BG
CP
CR
SH
AI
FI
PO
CO
AL
FOOD CATEGORY


FEMALE
PERCENTAGE
0
10
20
30
40
50
UN
BG
CP
CR
SH
AI
FI
PO
CO
AL
FOOD CATEGORY

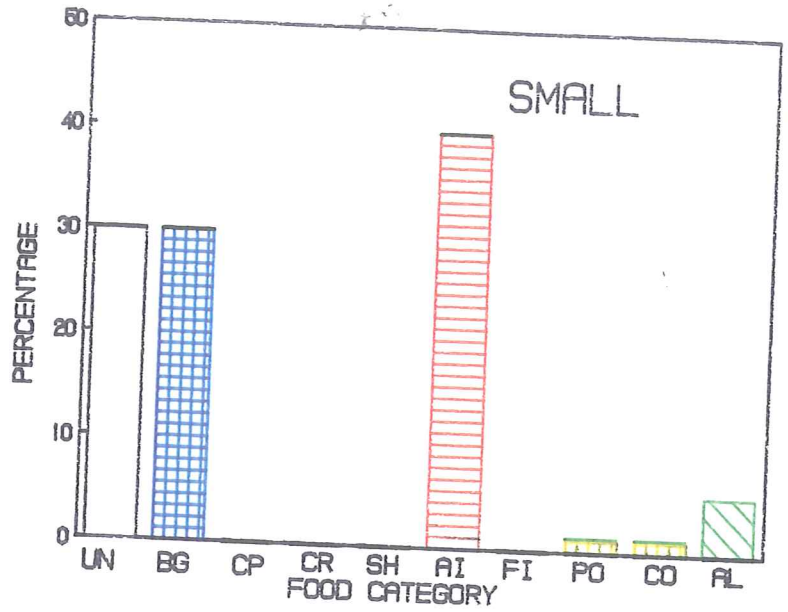
With respect to crab size, no significant differences in diet was observed between 40-60, 61-100 and 100-160 mm carapace width size class crabs (X^2 = 25.9, df = 18, NS, Fig. 2.2). All crabs contained molluscs as principle prey type; however, 40-60 mm crabs ate considerably greater proportion of amphipods and isopods. Crab, fish and algal remains were found only in stomachs of larger crabs.

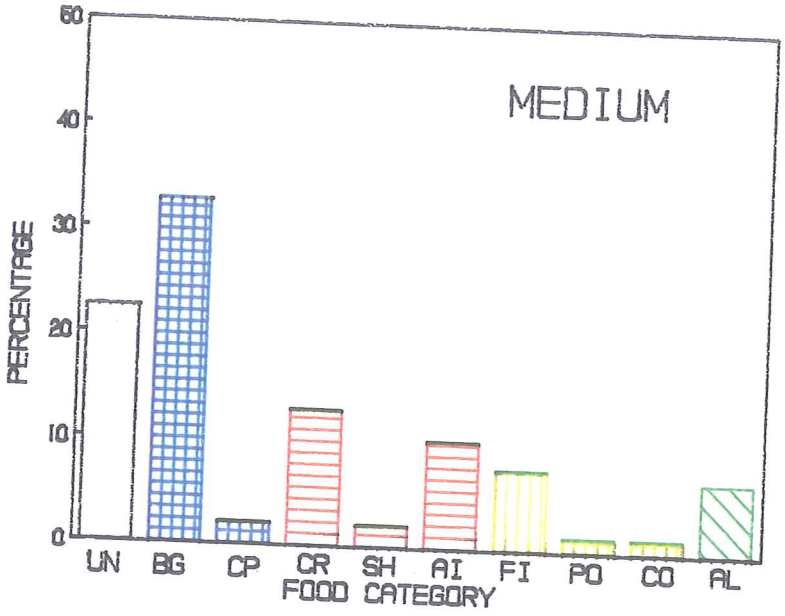
No clear seasonal pattern in dietary composition was evident during 1986 (X^2 = 32.06, df = 24, NS, Fig. 2.3). Molluscs, followed by Crustacea predominated during all seasons. However, cephalopods appeared only during summer, whereas shrimps and coelenterates occurred during spring. Porifera were absent from the diet during 1986.

Figure 2.2. Percentage frequency of occurrence for small (40.0-60.0 mm carapace width, n=31), medium (61.0-100.0 mm, n=82) and large (101.0-160.0 mm, n=54) crabs collected between June 1985 and April 1987.

KEY

UN = Unidentified material.
BG = Bivalves and gastropods.
CP = Cephalopods.
CR = Crabs.
SH = Shrimps.
AI = Amphipods and Isopods.
FI = Fish.
PO = Porifera.
CO = Coelenterates.
AL = Algae.


SMALL
PERCENTAGE
0
10
20
30
40
50
UN
BG
CP
CR
SH
AI
FI
PO
CO
AL
FOOD CATEGORY


MEDIUM
PERCENTAGE
0
10
20
30
40
50
UN
BG
CP
CR
SH
AI
FI
PO
CO
AL
FOOD CATEGORY

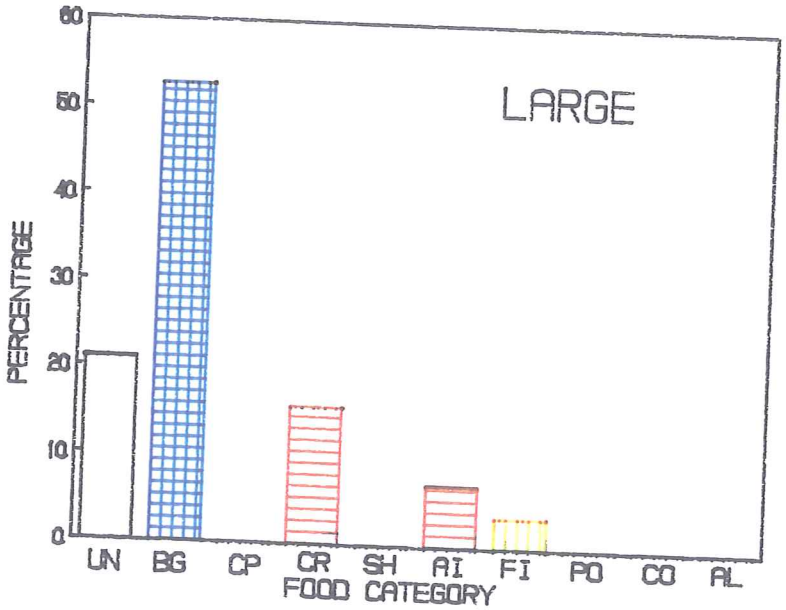
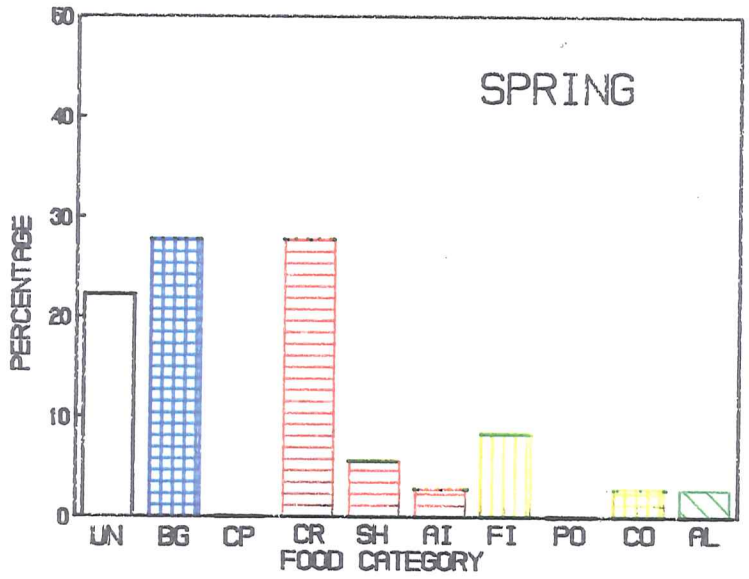
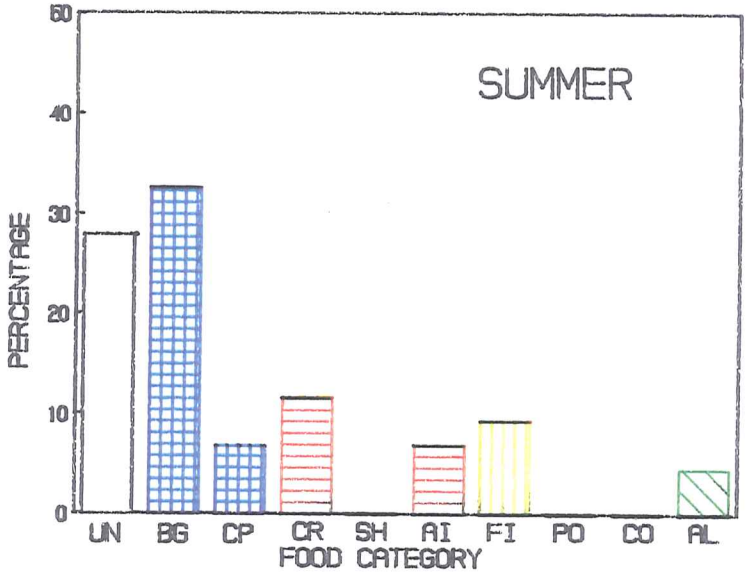

LARGE
PERCENTAGE
0
10
20
30
40
50
60
UN
BG
CP
CR
SH
AI
FI
PO
CO
AL
FOOD CATEGORY

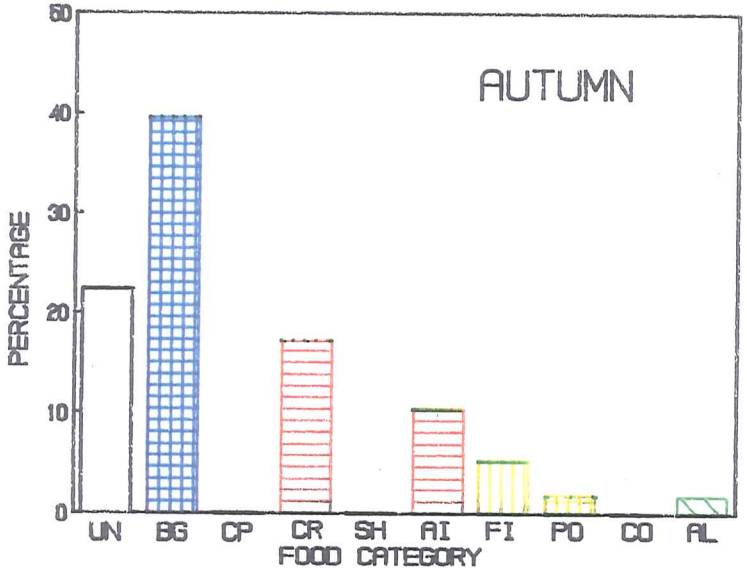
Figure 2.3. Percentage frequency of occurrence for crabs collected during Spring (Sep-Nov, n=31, top left), Summer (Dec-Feb, n=28, top right), Autumn (Mar-May, n=25, bottom left) and Winter (Jun-Aug, n=22, bottom right) 1986. Sexes combined.

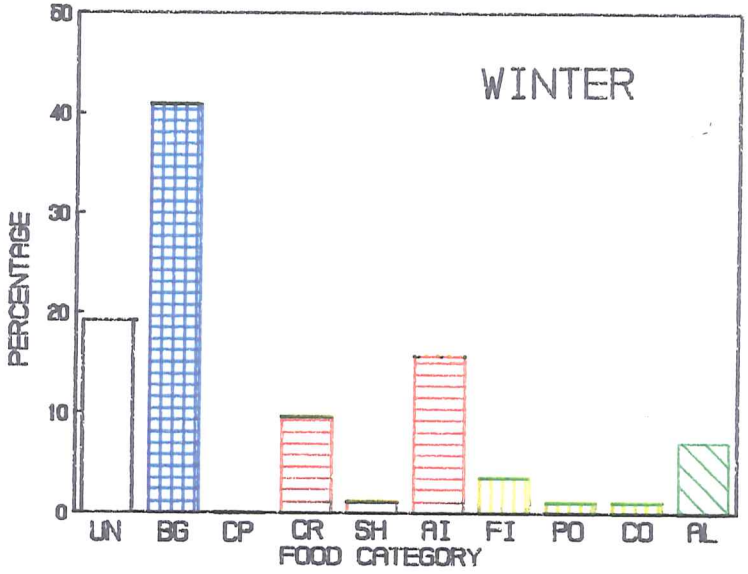
KEY

UN = Unidentified material.
BG = Bivalves and gastropods.
CP = Cephalopods.
CR = Crabs.
SH = Shrimps.
AI = Amphipods and Isopods.
FI = Fish.
PO = Porifera.
CO = Coelenterates.
AL = Algae.


SPRING
PERCENTAGE
0
10
20
30
40
50
UN BG CP CR SH AI FI PO CO AL
FOOD CATEGORY


SUMMER
PERCENTAGE
0
10
20
30
40
50
UN BG CP CR SH AI FI PO CO AL
FOOD CATEGORY


AUTUMN
PERCENTAGE
0
10
20
30
40
50
UN BG CP CR SH AI FI PO CO AL
FOOD CATEGORY


WINTER
PERCENTAGE
0
10
20
30
40
50
UN BG CP CR SH AI FI PO CO AL
FOOD CATEGORY

DISCUSSION

The analysis of stomach contents revealed Cancer novaezelandiae to be an generalized predator feeding on sessile and slow-moving benthic macro-invertebrates. Bivalve/gastropod molluscs, and crustacea formed the major constituents of diet. This trend was confirmed by both points and frequency occurrence methods. Fish, sponges, coelenterates formed only minor components of diet, and algae was also relatively unimportant.

The high incidence of animal material suggests that C.novaezelandiae is a predator of epi and infaunal prey. However, despite its predatory abilities, if the opportunity arose, it might would be expected to scavenge on incapacitated or decaying material. The absence of motile animals from the diet may reflect the crab's sedentary foraging nature.

Most authors agree that crabs feed on a wide variety of food types, both animal and plant matter (Scarratt & Lowe, 1972; Hill, 1976; Gotshall, 1977; Hill, 1979a; Feder & Paul, 1980; Elner, 1981; Paul, 1981; Stevens, Armstrong & Cusimano, 1982; Williams, 1982; Choy, 1986; Wear & Haddon, 1987). However, as in this study of C.novaezelandiae, most conclude that diet is dominated by molluscan and crustacean prey.

Cancer crabs have been shown to feed predominantly on molluscs and crustaceans. Other prey types form only minor components of the diet. The Dungeness crab Cancer magister preyed

primary on small bivalves (< 10 mm shell length), notably the clam Spisula polynyma which was observed in 48% of stomachs, whereas crustaceans occurred in 30% of stomachs (Feder & Paul, 1980). Gotshall (1977) examined C.magister from northern California, USA and found crabs fed primary on clams (56.1%) and amphipods/isopods (23.6%). Other prey items including hydroids, polychaetes, cephalopods, echinoderms and fish were found to be only minor components of diet. C.magister from British Columbia, Canada, also fed principally on crustaceans (59%) and clams (56%, Butler, 1954 cited in Gotshall 1977). Cancer irroratus was also found to be a predator of molluscs and found to eat 5-6 scallops per day (Elner & Jamieson, 1979).

Fish was also a common prey item of cancer crabs. C.magister collected from Grays Harbour, Washington State, USA, contained fish remains recorded in 11% of stomachs (Steven, Armstrong & Cusimano, 1982). Gotshall (1977) recorded fish remains in 24% of stomachs of C.magister and observed that crabs were capable of capturing juvenile fish that come into range. In the present study of C.novaezelandiae 6.8% of food items found consisted of fish remains. These belonged to the family Pleuronectidae and it is probable that much of the fish eaten is through scavenging of dead or dying fish and waste products thrown overboard by fishermen. There is no evidence of active predation on live adult fish either in the field or in the laboratory.

Plant material constitutes only a minor fraction of crab diet in cancer crabs. Only 2.4% and 3.9% of stomachs of C.magister and

C.irroratus, respectively, contained plant material comprising entirely of eelgrass Zostera marina (Gotshall, 1977; and Scarratt & Lowe, 1972). In the present study 5.5% of food items were of plant matter comprised of red, green and brown algae. Although Callinectes sapidus has been reported to eat living plants (Darnell, 1958 cited in Paul, 1981), it is not known if cancer crabs selectively feed on plant material, or merely accidentally ingest it with other food items.

For some crab species, annelids form a considerable proportion of the diet (Scarratt & Lowe, 1972; and Feder & Paul, 1980). Scarratt & Lowe recorded 19% occurrence of annelids, particularly nereids and polynoid polychaetes from stomachs of C.irroratus from Northumberland Strait, Gulf of St. Lawrence. C.novaezelandiae from the Avon-Heathcote Estuary were reported to contain remains of worms (Thompson, 1930). However crabs collected from nearby Lyttelton Harbour in this study did not eat annelids, despite their presence in the harbour benthos (Knight, 1971). This may reflect some degree of food type selection.

For some portunid crabs it has been shown that diet of male and female crabs differs significantly (Ropes, 1968, Elner, 1980). Male Liocarcinus puber were found to feed on a greater proportion of molluscs than did females. Choy (1986) concluded that these differences reflected cheliped strength, as male portunids possess larger, stronger chelae than females. Hence males are capable of feeding on a greater size range of molluscs. Cancrid crabs, however, exhibit homeochely. Both males and females

possess similar size chelae and thus may be expected to feed on the same prey types. It is not surprising therefore, that no variation was found in diet with respect to sex in C.novaezelandiae. Stevens, Armstrong & Cusimano (1982) also found a lack of sexual variation in diet for C. magister.

Differences in diet composition with crab size classes have been frequently reported (Gotshall, 1977; Feder & Paul, 1980; Paul, 1981; Stevens, Armstrong & Cusimano, 1982; Choy, 1986). Estuarine C.magister were shown to undergo distinct ontogenetic changes in food preference with age (Stevens, Armstrong & Cusimano, 1982). Bivalves dominated the diet of first-year benthic crabs (15-60 mm carapace width), with Crangon spp. dominating during the second year (61-100 mm). Older crabs (101-162 mm) switched to fish material as the principle prey. Butler (1954, cited in Gotshall 1977) noted that small C.magister (<100 mm) fed mostly on crustaceans, while large crabs (101-165 mm) switched to clams as preferred prey. C.magister from British Columbia showed a change from clams to fish after reaching a size of approximately 150 mm carapace width (Gotshall, 1977). Ropes (1968) observed plant and soft-shelled animals were most frequent in the stomachs of small Carcinus maenas (< 30 mm carapace width). Prey found included Spartina and small arthropods and insects. Adults, however, contained hard-shelled foods notably molluscs. In the present study no changes in diet composition were found for C.novaezelandiae between 40-135 mm carapace width. The three size classes of postmetamorphosis benthic crabs exhibited the same food types in relatively similar proportions.

The overlap in diet between size classes observed in the present study is surprising. Ontogenetic changes are considered to be a general phenomenon for cancrid crabs, particularly C.magister (Stevens, Armstrong & Cusimano, 1982), and are believed to be a direct result of mechanical constraints related to body size. Larger crabs have greater crushing capabilities, hence, are capable of feeding on a greater diversity of food types of a wider size range than smaller, weaker crabs. It has also been suggested that ontogenetic change decreases competition between age classes that occupy overlapping territory by partitioning food resources according to predator size (Pyke, Pulliam & Charnov, 1977). However, the similarity of dietary composition in C.novaezelandiae from Lyttelton Harbour may be the result of crabs feeding in an area of high food abundance. Thus crabs of all sizes feed on the same prey items in similar proportions, despite larger crabs utilizing larger prey due to stronger crushing abilities.

Seasonal variations in diet have been reported for portunid crabs (Elner, 1981; Paul, 1981; Choy, 1986). It is generally assumed that seasonal changes reflect availability of prey organisms throughout the year. The peak in abundance of bivalves in stomachs of Liocarcinus holsatus during autumn coincided with high bivalve densities. Moreover, high abundance of copepods during late spring and early summer coincided with high occurrence within fore-guts (Choy, 1986). Callinectes arcuatus was found to feed on molluscs throughout the year (Paul, 1981),

but highest mollusc predation corresponded to a peak in mollusc density during the dry season.

No seasonal variation was evident in the diet of C.novaezelandiae. All food categories occurred in similar proportions in the diet throughout the year. However, bivalves and gastropods showed peaked occurrence during winter, whilst crab remains peaked during spring. The high occurrence of molluscs during winter corresponded with a similar high molluscan occurrence in the diet of L.holsatus and L.puber (Choy, 1986).

Cannibalism is a common feature in some decapods (Scarratt & Lowe, 1972; Gotshall, 1977; Stevens, Armstrong & Cusimano, 1982; Choy, 1986), and probably reflects the opportunistic predatory nature of crabs. Fragments of small C.novaezelandiae were frequently found in stomachs of adult crabs. Cannibalism is most likely to occur when small juveniles and soft, newly moulted crabs are encountered. Such encounters have been observed in the laboratory. Cannibalism may occur for two main reasons: Crabs may form an important food resource, or they may provide the increased calcium intake necessary to strengthen the newly formed exoskeleton of moulted crabs (Williams, 1982). Cannibalism may therefore act as an effective density-dependent mortality factor (Klein-Breteler, 1975 cited in Elner, 1981). Cannibalism is likely to be greatest during periods of recruitment of post-larvae, a time when large crabs prey heavily on smaller, newly recruited crabs, and thus may seriously influence population structure. In the present study fragments of small

C.novaezelandiae were frequently found in stomachs of adult crabs suggesting that cannibalism may have a direct influence on the population structure within Lyttelton Harbour.

Most authors suggest that composition of crab diet reflects food availability in the surrounding benthos. This supports the belief that crabs with opportunistic tendencies show very little selection. Knox (1983) recorded 16 species from within the benthos of Lyttelton Harbour. Species included one nematode, nine polychaetes, two crustaceans and one bivalve. Density of animals ranged from 496-2088 m^{-2}. Knight (1971), however, found a considerably greater number of species which included 42 mollusc (18 bivalve, 19 gastropod and 2 cephalopod species), 24 arthropod (9 decapod species) and 29 annelid (27 polychaete species). Also recorded in the benthos were various echinoderms, brachiopods, ectoprocts and coelenterates. Biomass of 7000 to 9000 grams m^{-2} have been estimated for C.stutchburyi alone. Despite discrepancies between the two studies, it appears that a wide array of food types is available from within the benthos. The present study has found that C.novaezelandiae from Lyttelton Harbour does feed on a wide range of prey items and thus like previous studies can be considered opportunistic, but with distinct preferences for mollusc and crustacean species. These preferences may be the result of high mollusc and crustacean densities occurring within Lyttelton Harbour. Chatterton (pers. comm.) found that C.novaezelandiae undertakes regular foraging excursions into the intertidal zone associated with night-time

high tide cycles. These excursions may be to feed on mollusc and crustacean prey which are abundant in the intertidal region.

A selective advantage will be conferred to those crabs which are capable of feeding on a diverse range of prey species. This is because competition for food at both intra and interspecific levels is reduced. This lack of competition will allow high densities of crabs to be maintained within the habitat. It is not known at present how much food C.novaezelandiae consumes under natural conditions; however, laboratory studies suggest that it can consume prey in relatively high numbers (see Chapter Four). Therefore its large size and abundance in Lyttelton Harbour makes it an important predator of molluscs and crustaceans, and it may as Muntz et.al. (1965) suggests for Cancer pagurus and Carcinus maenas play an important factor in determining the distribution of prey species. However, this aspect of its ecology is virtually unknown.

CHAPTER THREE

FUNCTIONAL MORPHOLOGY OF THE FEEDING APPARATUS

INTRODUCTION

Crabs exhibit a wide diversity of dietary tendencies ranging from macrophagous omnivores to filter and deposit feeders. Therefore, it might be expected that the morphology of the feeding apparatus, that is the mouthparts, gastric mill and chelipeds, are functionally related to diet. Some crabs are specialists feeding on one particular prey type. Consequently their feeding apparatus tends to be specialized in structure (Shoup, 1968; Bertness and Cunningham, 1981). For example, the third maxillipeds and secondary antennae of suspension feeders Petrolisthes elongatus (Porcellanidae) and Emerita analoga (Hippoidea) are large and well endowed with setae allowing rapid straining of material from the adjacent water (Weymouth & Richardson, 1912 cited in Wenner, 1977; Scott, 1958; Schembri, 1982). However, the majority of crabs are generalists, feeding on a wide variety of food types of both animal and plant origin, and would be expected that their feeding apparatus is unspecialised in structure.

Few studies have attempted to investigate functional morphology of the feeding apparatus and the relationship between morphology and diet. Such studies have paid particular attention to anomurans, particularly hermit crabs (Scott, 1958; Kunze and

Anderson, 1979). Many studies have investigated the predatory abilities of macrophagous crabs (Elner, 1978; Williams, 1978; Hill, 1979a; Seed, 1980; Chilton and Bull, 1986; Davidson, 1986); however, these studies have concentrated on food capture and food manipulation using the chelipeds, without reference to the structure or function of the mouthparts and gastric mill.

The only significant studies of macrophagous brachyurans with regard to the feeding apparatus are those of Ebalia tuberosa (Schembri, 1982), Scylla serrata (Barker and Gibson, 1978), Ozius truncatus and Leptograpsus variegatus (Skilleter and Anderson, 1986). Surprisingly, little attention has been paid to crabs belonging to the family Cancridae despite their conspicuous nature. Pearson (1908) provides an extensive morphological description of Cancer pagurus, yet no information is provided regarding the functional aspect of the feeding apparatus. To date, there is no information describing the morphology or growth of the chelipeds, structure of mouthparts and gastric mill of Cancer novaezelandiae. The functional aspects of the feeding apparatus has yet to be investigated.

The feeding apparatus of brachyurans show discontinuous growth patterns with the calcified structures of the chelae, mouthparts and the ossicles of the gastric mill being regularly replaced during moulting. Thus the feeding apparatus, particularly the chelipeds may exhibit different rates of growth relative to other parts of the body; this phenomenon has been termed relative or allometric growth (Huxley, 1932), which has

been extensively documented (Weymouth and MacKay, 1936; Bennett, 1974; Hartnoll, 1974; Jones, 1978; Haefner Jr., 1981; Simons, 1981; Davidson and Marsden, 1987). Studies show that the chelipeds tend to exhibit negative allometric growth (chelae grow slower relative to the carapace) or positive allometric growth (chelae grow faster than the carapace; Weymouth and Mackay, 1936; Haley, 1969; Jones, 1978). Other species show isometry of the chelae (Hartnoll, 1982). Also, differences in chela growth between sexes are commonly observed. Furthermore, few crabs show a constant rate of growth of the chela throughout the life cycle. Instead growth tends to increase dramatically after the pubertal moult particularly in males. Hence, cheliped dimorphism with respect to crab size and sex is a common feature of portunid, grapsid, ocypodid, parthenopid and xanthid crabs. Since the chelae are the principle structures of prey manipulation and mastication, it would be expected that differential growth of the chelae will have a profound effect on diet (see Chapter Two with regarded to ontogenetic changes and diet). However, no one has examined the intraspecific morphological relationship of feeding apparatus and dietary composition.

This study examines the functional morphology of the feeding appendages of C.novaezelandiae. The aim of the work is to examine the morphology of the chelae, mouthparts and gastric mill of different size individuals; and to investigate chelae growth with respect to crab size and sex.

MATERIALS AND METHODS

All crabs collected during the diet sampling programme were used to examine the feeding apparatus. Individuals with missing or regenerated appendages were not included. In the laboratory, the sex of each crab was noted and the following measurements were made to the nearest 0.1 mm using Vernier calipers: carapace width (CW), measured at the widest part; chela propodus height (CHH), from the tip of the large dorsal spine to the base of the chela; and chela propodus length (CHL), from base to tip of the propodus along the ventral margin (Figure 3.1). Carapace width was used as the reference dimension.

Relative growth of the chelae was examined mathematically using the allometric growth equation:

$$Y = aX^b$$

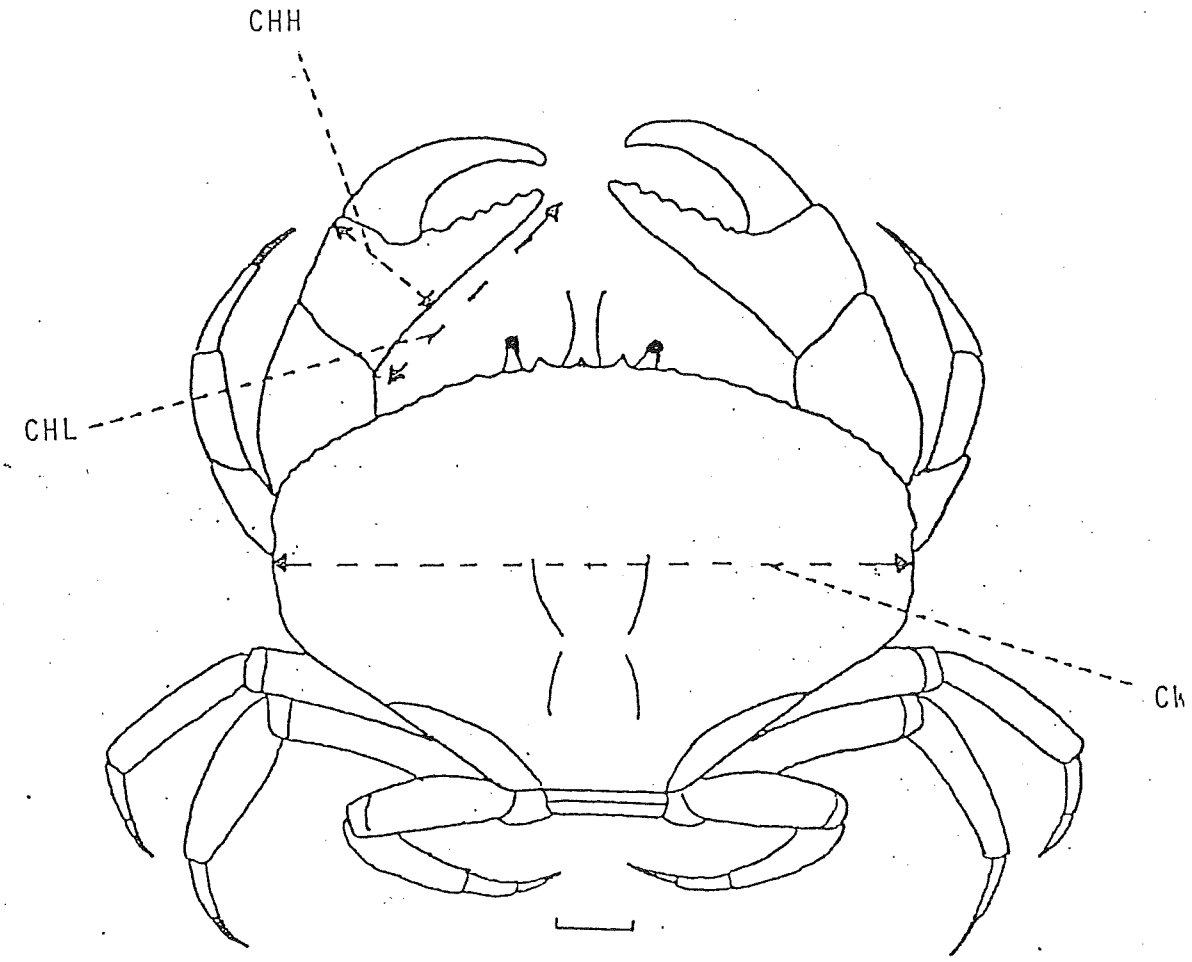
were Y and X are morphological dimensions and a and b are growth constants.

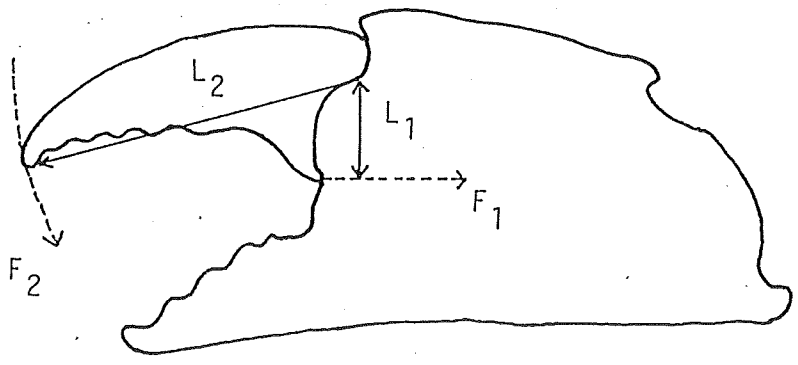
The logarithmic transformation $\log Y = a\log X + \log b$ linearises the equation to best describe empirically patterns of growth. A slope of $b < 1$ indicates negative allometry, while a slope of $b > 1$ indicates positive allometry. Where the slope of the line does not differ significantly from 1, there is isometry, and both structures grow at the same rate. This method of growth analysis has been extensively used in previous studies of brachyuran

Figure 3.1. Dimensions used in measurements of carapace and chelae.

Top. CW = Carapace width.
CHH = Propodus Height.
CHL = Propodus Length.

Bottom. L_1/L_2 = Mechanical advantage.
The dotted arrows indicate the directions through which forces F_1 and F_2 act.


CHH
CHL
CW


L2
L1
F1
F2

growth (Huxley, 1932; Hartnoll, 1974, 1978; Haefner Jr., 1981; Davidson and Marsden, 1987). Regression lines were fitted using the Least Squares Regression (Model I) procedure following natural logarithmic transformations. Student t-tests were performed on slope and y-intercept to compare regression lines between left and right chela and for male and female crabs using a 5% level of significance. All slopes were tested against 1.0 using t-tests.

The mouthparts, gastric mill and chela were removed from five male and five female specimens of two size classes (60.0-70.0 and 120.0-130.0 mm carapace width) These were drawn under a stereo-microscope with the aid of a Camera Lucida. The relationship between mouthpart size and crab size was investigated using length/width ratio of basi-ischiopodite and endopod of the third and second maxilliped respectively.

Feeding observations were made of different sized crabs placed within glass aquaria and fed small pieces of fresh mussel Mytilus edulis aoteanus.

Mechanical properties of the chelipeds were examined with respect to crab size and sex. In a frictionless lever system, the torque applied to the system (F_1L_1) is equal to the torque applied by the system (F_2L_2); were F_1 is the input force, F_2 is the output force, and L_1 and L_2 are respective lever lengths. In such a system, the ratio of forces (F_2/F_1), the "ideal mechanical advantage", is numerically equal to the ratio of lever arm length

(L_1/L_2). This ratio of lever length is considered to be the "mechanical advantage" (MA). Thus the force produced by the system increases with a increasing L_1/L_2 ratio, and thus MA is a good indication of the amount of stress applied by the lever system (Brown, Cassuto and Loos, 1979). The mechanical properties of the chelae were investigated by examining the L_1/L_2 ratio. L_2 was considered the distance from the pivot to the tip of the dactylus, and L_1 as the distance between the pivot and the point of insertion of the dactylus of the closer muscle apodeme (Figure 3.1). This procedure has proved to successfully describe the mechanical properties of brachyuran chelipeds in previous studies (Warner and Jones, 1976; Vermeij, 1976; Brown, Cassuto and Loos, 1979).

Correlations of left and right MA and crab size were obtained. Comparisons of mean MA between left and right chela and sex were made using Student t-tests using a 5% level of significance.

RESULTS

Structure of mouthparts.

Apart from the disparity in size, there were no obvious structural differences between the same mouthparts from large (120.0-130.0 mm carapace width) and small (60.0-70.0 mm carapace width) crabs. Also no differences in basi-ischiopodite and endopod length/width ratios of the third and second maxilliped were observed (2.45, 4.12, 2.46 and 4.3 for third and second maxilliped of large and small crabs respectively). The mouthparts were held close to the body wall and, when the crab is not feeding, they were protected by the third maxillipeds. Flattening in the dorso-ventral plane was a prominent feature of the maxillipeds and maxillae. Thus, each mouthpart was characterised by a broad surface area. Although setae were present over the dorsal surfaces, setation was most dense along the margins of both maxillipeds and maxillae. Below are descriptions of the mouthparts (see Figure 3.2).

Third Maxilliped

Endopod : The basi- and ischium of the endopod are flattened dorsoventrally and fused to form a plate-like structure. The medial margin of the basi-ischium is fringed by a dense row of short setae and bears numerous blunt, rounded teeth known as the crista dentata. The distal portion of the meropodite is also flattened and articulates distally with the carpopodite. The three distal segments, particularly the terminal dactylopodite articulates freely and is sparsely covered with setae.

Figure 3.2. Mouthpart structure of C.novaezelandiae.

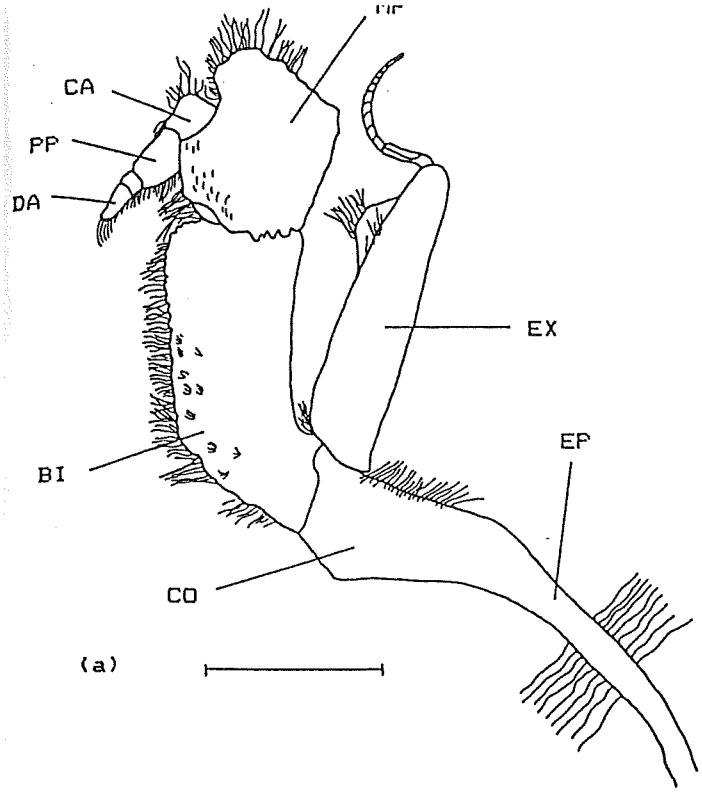
(a & d) Third maxilliped.
(b & e) Second maxilliped.
(c & f) First maxilliped.

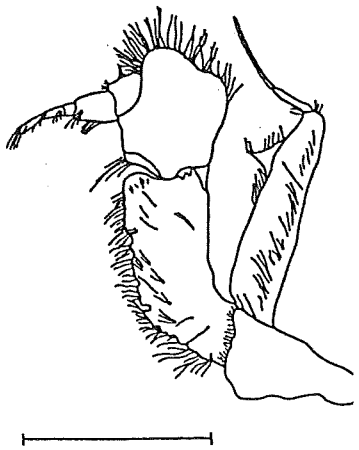
Large (121.3 mm carapace width) hard-stage male crab on left (a-c). Small (62.4 mm carapace width) hard-stage male crab on right (d-f).

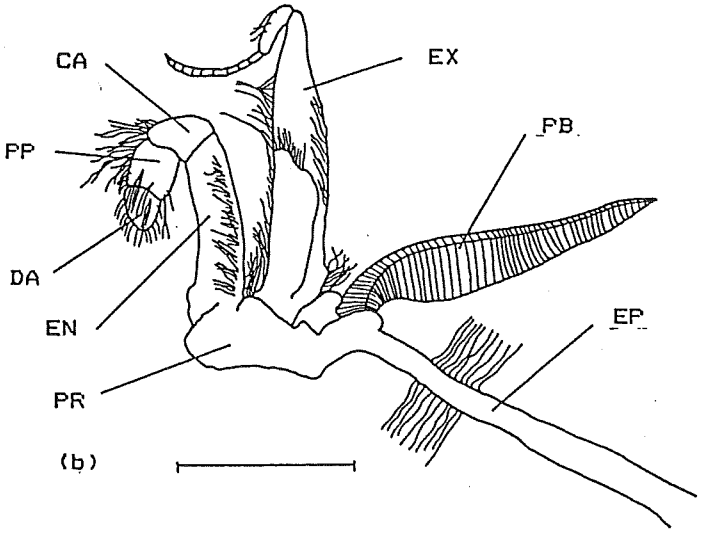
All mouthparts are right side, oral view. Scale bar = 10 mm.

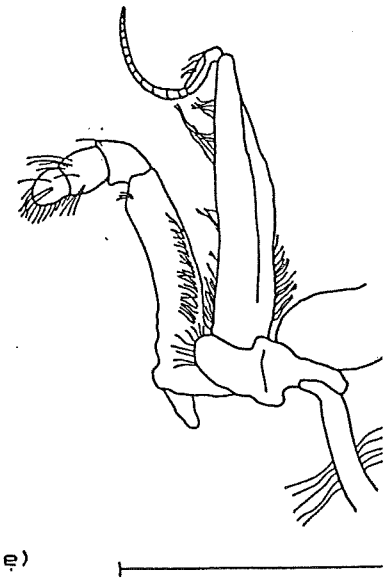
KEY

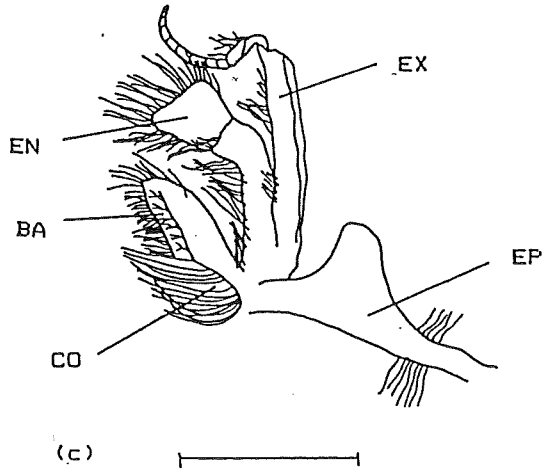
BA = Basipodite.
BI = Basi-ischiopodite.
CA = Carpopodite.
CO = Coxopodite.
DA = Dactylopodite.
EN = Endopodite.
EP = Epipodite.
EX = Exopodite.
MP = Meropodite.
PB = Podopodite.
PP = Propodite.
PR = Protopodite.


CA
PP
DA
EX
BI
EP
CO
(a)


(d)


CA
EX
PB
PP
DA
EN
EP
PR
(b)


(e)


EX
EN
BA
EP
CO
(c)

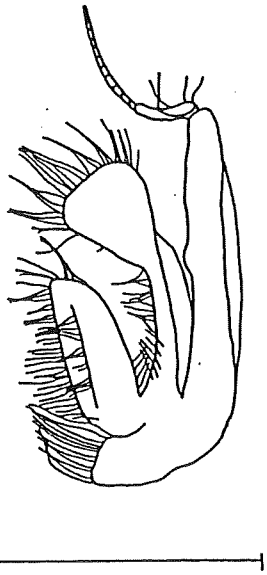

(f)

Figure 3.2. (Cont'd) Mouthpart structure of C.novaezelandiae.

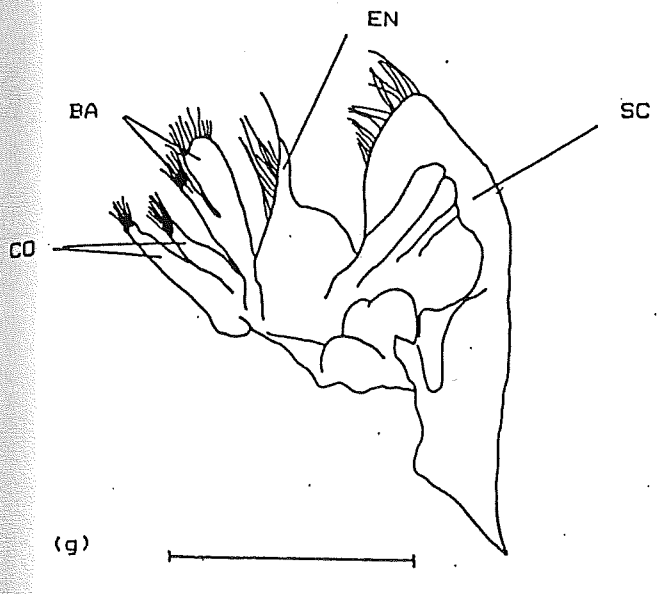
(g & j) Second maxilla;
(h & k) First maxilla;
(i & l) Mandibles.

Large (121.3 mm carapace width) hard-stage male crab on left (g-i).
Small (62.4 mm carapace width) hard-stage male crab on right (j-l).

All mouthparts are right side, oral view. Scale bar = 10 mm.

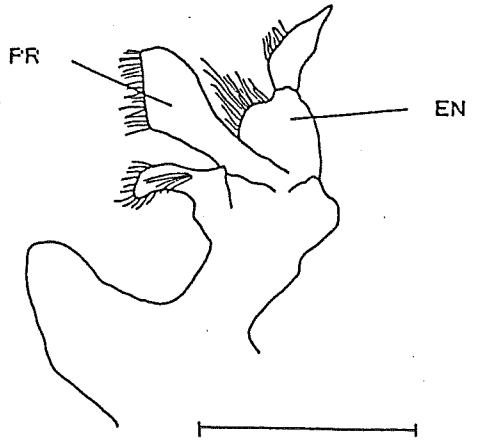
KEY

AP = Apophysis.
BA = Basipodite.
CO = Coxopodite.
EN = Endopodite.
SC = Scaphognathite.
PA = Palp.
PR = Protopodite.

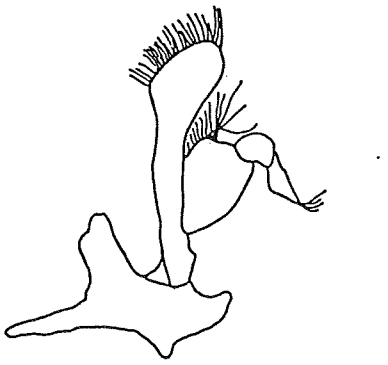


(g)

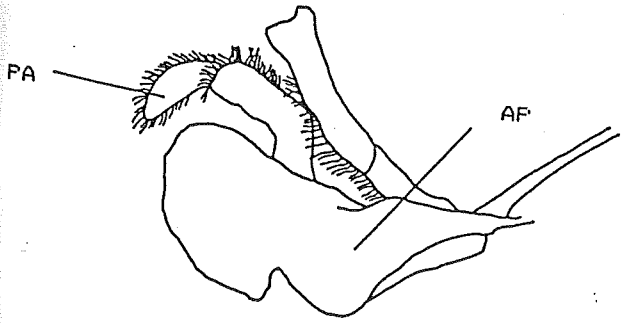
(j)



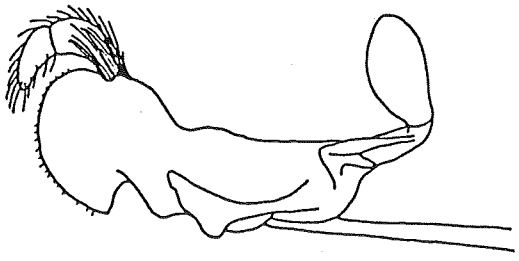
(h)



(k)



(i)



(l)

Exopod : The basal segment of the exopodite distal to the coxopodite interlocks with the basi-ischiopodal and meropodal sections of the endopod when in a resting position. The flexible terminal segment of the exopodite, lacking setae, is held posterior to the endopodal meropodite. The epipodite is covered extensively with long setae.

Second Maxilliped

The second maxillipeds bear a large podobranch arising from the coxopodite. Although reduced in size, the endopod is heavily setosed on the dorsal surface, but naked along the medial margin. The three distal endopodal segments are similar to those of the third maxilliped but the propodite and dactylopodite are densely covered with setae. The meropodite is fused with the ischiopodite which articulates freely with the basipodite which, in turn, is fused with the coxopodite. As with the third maxilliped, the epipodite is extensively covered with setae.

First Maxilliped

The basi- and coxopodites of the first maxillipeds are well developed and endowed with setae along their distal borders. The basipodite bear two rows of long setae; one on the medial edge and the other arising subterminally on the oral face. The endopodite which is distolaterally compressed, is fringed by long setae along its distal and medial margins. At rest the elongated exopodite, naked of any setation, is held close to the endopodite.

Second Maxilla

The scaphognathite dominates the second maxilla. Derived from the exopodite, it functions as a pump regulating water passage through the branchial chamber. The endopodite is rudimentary and consists only of a digitate projection from the edge of the feeding appendage. The basipodite and coxopodite segments are distally divided to form four separate membranous endites, each of which is fringed with small setae.

First Maxilla

The first maxilla arises immediately behind the mandible. It is a small structure comprised of a protopodite and endopodite. Long setae line the medial edge of the basipodite. The exopodite is absent.

Mandible

The mandible lies at the side of the mouth and is heavily chitinised. The main portion is an elongate strongly calcified structure which is divided into two parts; an inner part which acts as a jaw, and an outer part (the apophysis) to which are attached the tendons of the mandibular muscles. The inner region of the mandible is sharp and rounded, and lacks teeth along the margin of the incisor process. A mandibular palp arises dorsally from the apophysis of each mandible, with the palpal segment uniformly covered with setae around the periphery.

Structure of the fore-gut

The alimentary canal is composed of three distinct regions; the fore-, mid- and hind-gut. It extends from the mouth, situated on the cephalic region between the mandibles, to the anus on the telson.

The fore-gut is the site of primary physical degradation of ingested food. The fore-gut consists of two regions; a large anterior cardiac stomach, in which the oesophagus opens; and a smaller posterior pyloric stomach, which eventually leads to the mid-gut and digestive glands (Figure 3.3). These two regions were separated by a narrow constriction.

Cardiac-Stomach

The cardiac-stomach is a large, spherical dorsoventrally flattened sac. The walls are mostly membranous, however regions of the wall are thickened and calcified into plates or ossicles. The arrangement of these ossicles acts to form a complex grinding organ, the gastric mill. This is described below (See Figure 3.4).

Structure Of Gastric Mill.

The gastric mill contains three major ossicles. A single ossicle on the dorsal wall bears a single tooth, while on the lateral walls, a pair of ossicles also bear single teeth, known as the lateral teeth. In addition, smaller supportive ossicles are present. All ossicles are attached to muscles and together form a very effective apparatus for physically masticating food

Figure 3.3. Lateral view of the fore-gut of male (69.6 mm carapace width) hard-stage *C.novaezelandiae*.

Scale bar = 10 mm.

KEY

AGM = Anterior gastric muscle.
ALT = Accessory lateral teeth.
DT = Dorsal tooth.
LT = Lateral tooth.
UC = Urocardiac ossicle.
ZC = Zygocardiac ossicle.

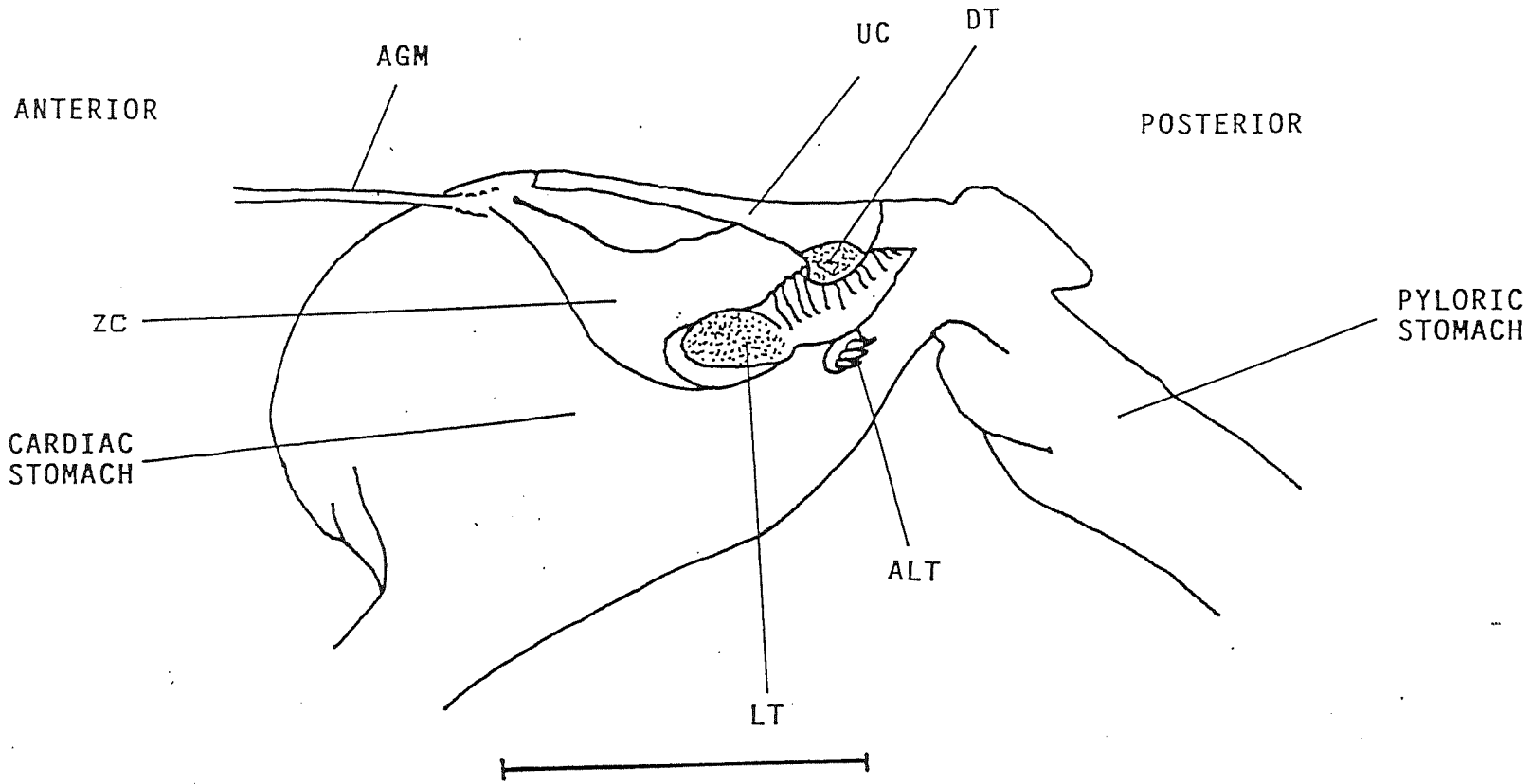
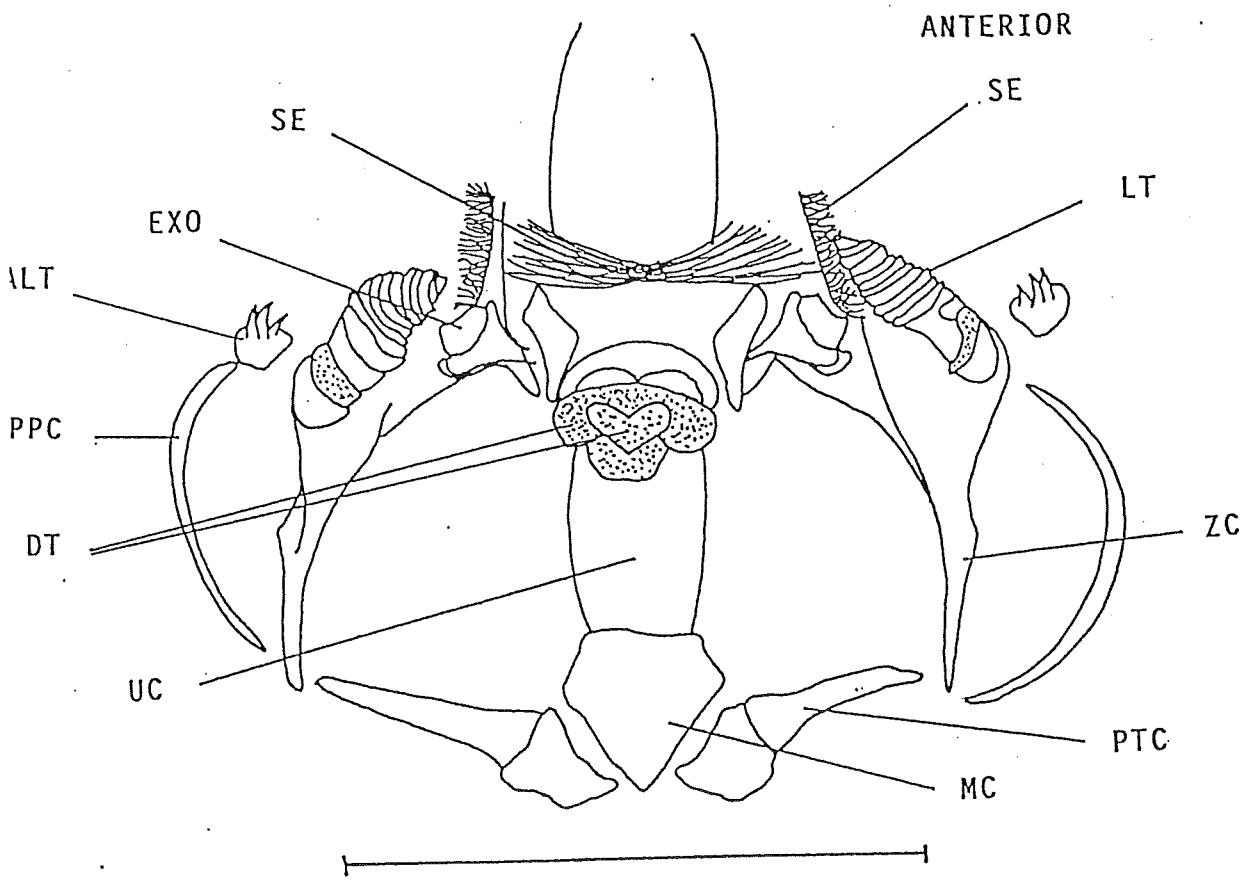

AGM
UC
DT
ANTERIOR
POSTERIOR
ZC
PYLORIC
STOMACH
CARDIAC
STOMACH
ALT
LT

Figure 3.4. Ventral views of dorsal surface of the cardiac-stomach. Lateral walls spread out (top), lateral tooth with accessory teeth behind (bottom).

KEY

ALT = Accessory lateral teeth.
DT = Dorsal tooth.
EXO = Exocardiac ossicle.
LT = Lateral tooth.
MC = Mesocardiac ossicle.
PPC = Pre=pectineal ossicle.
PTC = Pterocardiac ossicle.
SE = Setae.
UC = Urocardiac ossicle.
ZC = Zygocardiac ossicle.


ANTERIOR
SE
SE
LT
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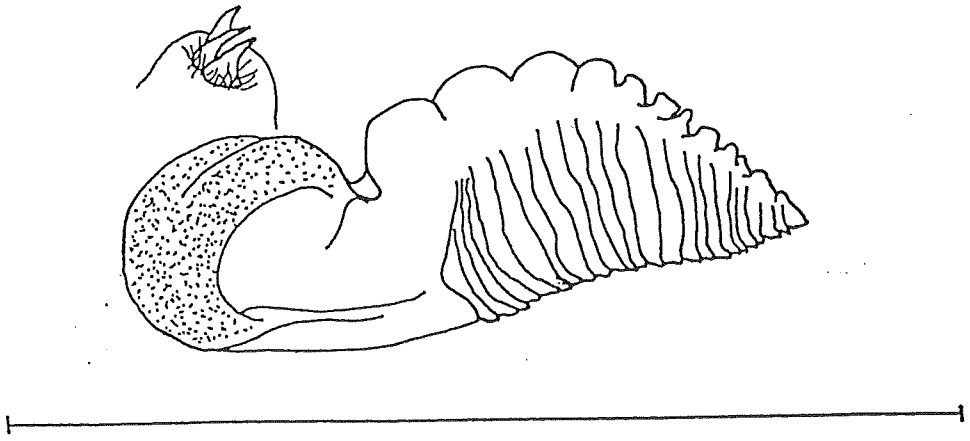
PPC
DT
ZC
UC
PTC
MC



which has passed into the cardiac-stomach. The ossicles of the cardiac-stomach are described below.

The Ossicles Of The Gastric Mill.

The ossicles of the gastric mill are arranged to form an complex integrated mechanical unit. The two lateral pterocardiac ossicles form the sides, while the single mesocardiac ossicle forms the keystone.

i] Mesocardiac Ossicle.

This is a small ossicle in the dorsal wall. It is a small, thick, triangular-shaped ossicle, with the apex pointing forwards. It is bounded laterally by pterocardiac ossicles with distinct separations between them. Attached to the mesocardiac ossicle is the urocardiac ossicle.

ii] Pterocardiac Ossicles.

These are paired and situated to the left and right of the mesocardiac. Each is a wedge-shaped plate running to the sides of the cardiac region. It is attached to the zygocardiac ossicle by a strong ligament.

iii] Zygocardiac Ossicles.

These are the stoutest ossicles of the gastric mill. Each passes back posteriorly and is attached to the exopyloric ossicle. In shape, the zygocardiac ossicle is triangular, rising to a thick plate, which is curved ventrally and lies parallel to the urocardiac ossicle. This plate appears "foot-like" in shape

bearing denticles as well as 15-20 small transverse ridges. This system of denticles and ridges constitute the lateral tooth. The thick chitinous covering of denticles and ridges is impregnated with brown pigment, giving it a yellow to brown appearance.

iv] Urocardiac Ossicles.

This is a large medial plate on the dorsal wall fused with the mesocardiac ossicle in front. It passes posteriorly as a long, thick rectangular plate, ending in a single, large blunt tooth which projects downwards, known as the dorsal tooth. Lying immediately behind is a dense single row of setae.

v] Exopyloric Ossicles.

These are a pair of small triangular plates lying posterior to the zygocardiac ossicle. Lying directly posterior and on either side is a row of dense setae.

vi] Pectineal Ossicles.

These are small paired ossicles, each lying anterior to the lateral tooth. On each of the ossicles are three claw-like teeth, known as lateral accessory teeth. The number of lateral accessory teeth remained the same in crabs of all sizes.

vii] Pre-pectineal Ossicles.

These are two elongated ossicles running on either side of the outer zygocardiac ossicle. The dorsal end is attached to the anterior region of the zygocardiac ossicle, while posteriorly it is attached to the pectineal ossicle.

The size of the cardiac-stomach increased with crab size. The structure of the gastric mill however, remained unchanged, although the number of transverse ridges of the lateral tooth appeared to increase with crab size. No structural differences between the sexes were observed.

Morphology, Growth and Mechanical Advantage Of The Chelae.

Structure.

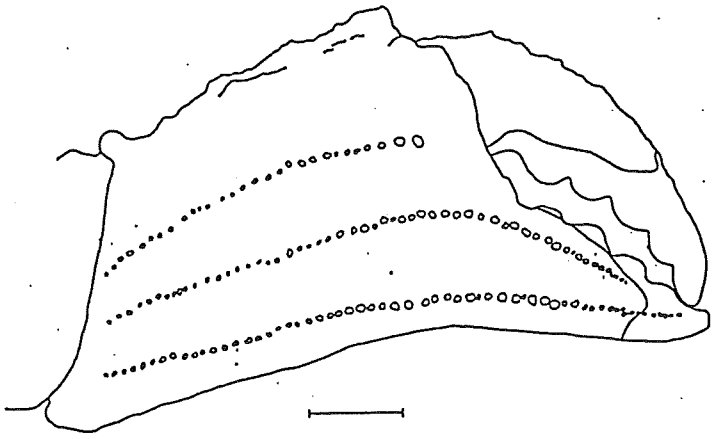
Male and female chelae showed monomorphoism or homeochely with the left and right chelipeds being similar in size, structure and dental pattern. No differences were observed with respect to chela dental pattern between males and females and different sized crabs (Figure 3.5). The occlusive surfaces of the chela bear 4-5 discrete, blunt, molariform teeth on both the dactylus and propodus. Adjacent to the molar teeth lie a sharp distal tooth on both fingers. When the chela is closed, these distal tips come into contact; however, no contact is made between the molar teeth of the dactylus and propodus. Hence during claw closure a relatively large gape exists.

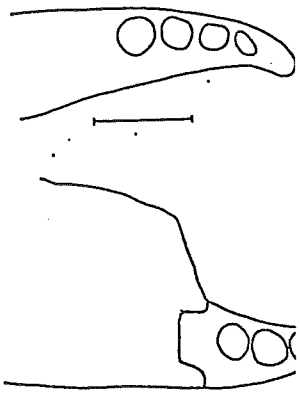
Growth

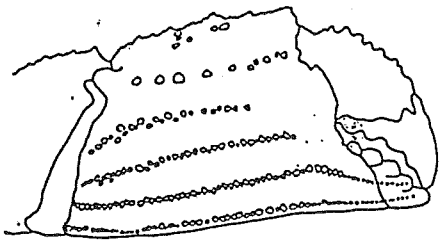
Allometric growth equations of propodus height and length is shown in Table 3.1. Relative growth of the left and right propodus height and length for male and female crabs were not significantly different (Table 3.2, Figures 3.6 & 3.7). No sexual differences were found between crabs of similar size with respect to propodus growth rate (Table 3.3). Propodus height

Figure 3.5. Lateral view of right chela of male C.novaezelandiae (121.9 mm carapace width, top; and 62.4 mm, bottom) with occlusive surfaces of dactyl (above) and propodus (below).

Scale bar = 10 mm.







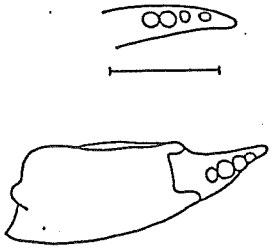


Table 3.1. Linear constants of the regression equations for relative growth the chelae in male and female *C.novaezelandiae*.

$$Y=aX^b$$

a = Y-Intercept, b = Slope, Se(b) = Standard Error of the Mean,
r^2 = Correlation Coefficient, N = Sample Size,
t = Slope Tested Against 1,
A.S. = Allometric Status.

Dimension	a	b	Se(b)	r^2	N	t	A.S.
MALE							
Left Propodus Height	-2.0019	1.132	0.0117	0.98	166	11.3	+
Left Propodus Length	-1.0987	1.083	0.0085	0.99	165	9.86	+
Right Propodus Height	-2.0623	1.147	0.0094	0.99	160	15.6	+
Right Propodus Length	-1.0780	1.079	0.0077	0.99	159	10.3	+
FEMALE							
Left Propodus Height	-2.0043	1.125	0.0338	0.93	79	3.70	+
Left Propodus Length	-1.0217	1.052	0.0259	0.96	78	2.01	+
Right Propodus Height	-1.9429	1.1128	0.0277	0.96	76	4.07	+
Right Propodus Length	-1.0751	1.0662	0.0261	0.96	77	2.54	+

Table 3.2. Comparison of linear constrants of regression equations of the propodus in male and female *C.novaezelandiae*.

MALE

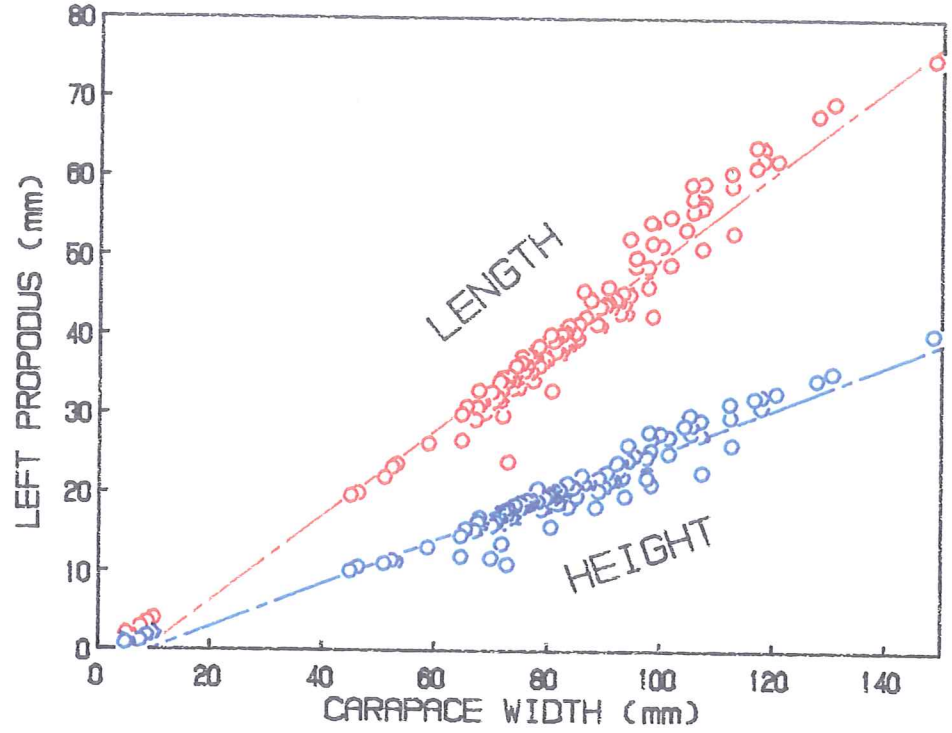
Left vs Right Propodus Height	t	df	N	
Y-Intercept	0.922	1	326	NS
Slope	0.950	1		NS
Left vs Right Propodus Length				
Y-Intercept	0.410	1	324	NS
Slope	1.759	1		NS
FEMALE				
Left vs Right Propodus Height				
Y-Intercept	0.327	1	155	NS
Slope	0.280	1		NS
Left vs Right Propodus Length				
Y-Intercept	0.478	1	155	NS
Slope	0.546	1		NS

Figure 3.6. Relationship between chela propodus height and length and carapace width for male C.novaezelandiae.

Top. Left chela (n=165 and n=166 for height and length respectively).

Bottom. Right chela (n=159 and n=160 for height and length respectively).

Regression equations are given in Table 3.1.


LEFT PROPODUS (mm)
CARAPACE WIDTH (mm)
LENGTH
HEIGHT
0
10
20
30
40
50
60
70
80
0
20
40
60
80
100
120
140

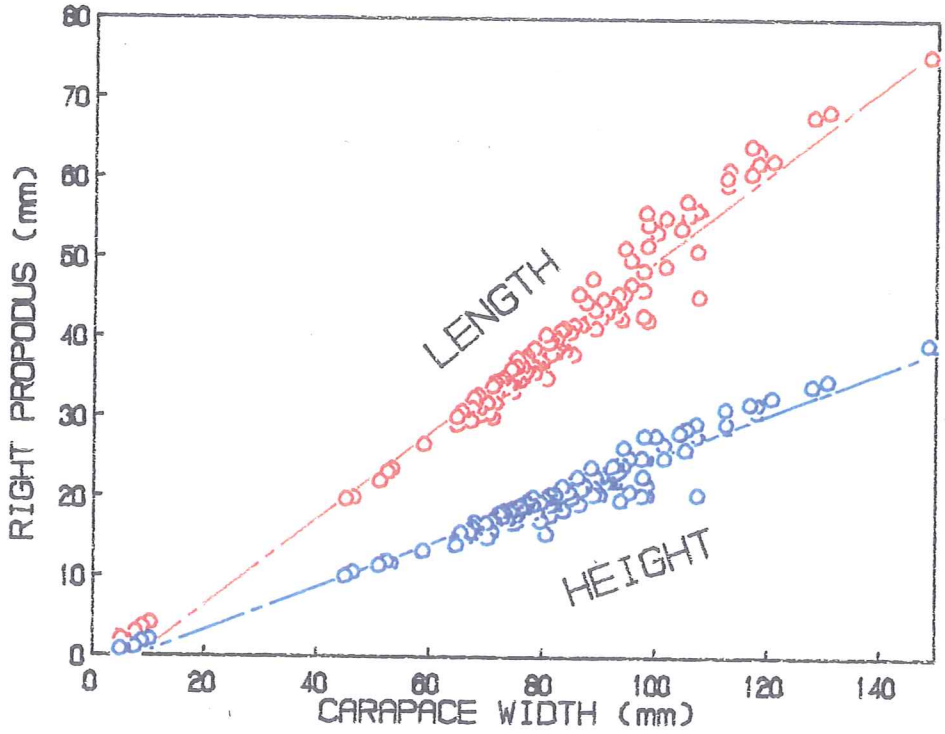
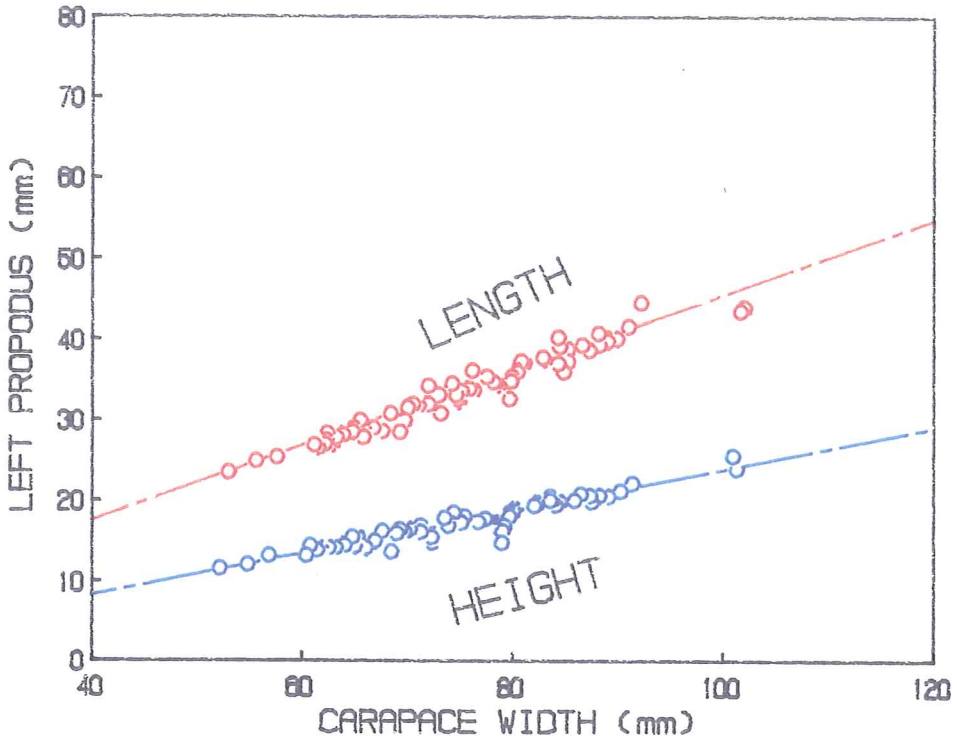

RIGHT PROPODUS (mm)
CARAPACE WIDTH (mm)
LENGTH
HEIGHT
0
10
20
30
40
50
60
70
80
0
20
40
60
80
100
120
140

Figure 3.7. Relationship between chela propodus height and length and carapace width for female C.novaezelandiae.

Top. Left chela (n=78 and n=79 for height and length respectively).

Bottom. Right chela (n=77 and n=76 for height and length respectively).

Regression equations are given in Table 3.1.


LEFT PROPODUS (mm)
0
10
20
30
40
50
60
70
80
LENGTH
HEIGHT
40
60
80
100
120
CARAPACE WIDTH (mm)

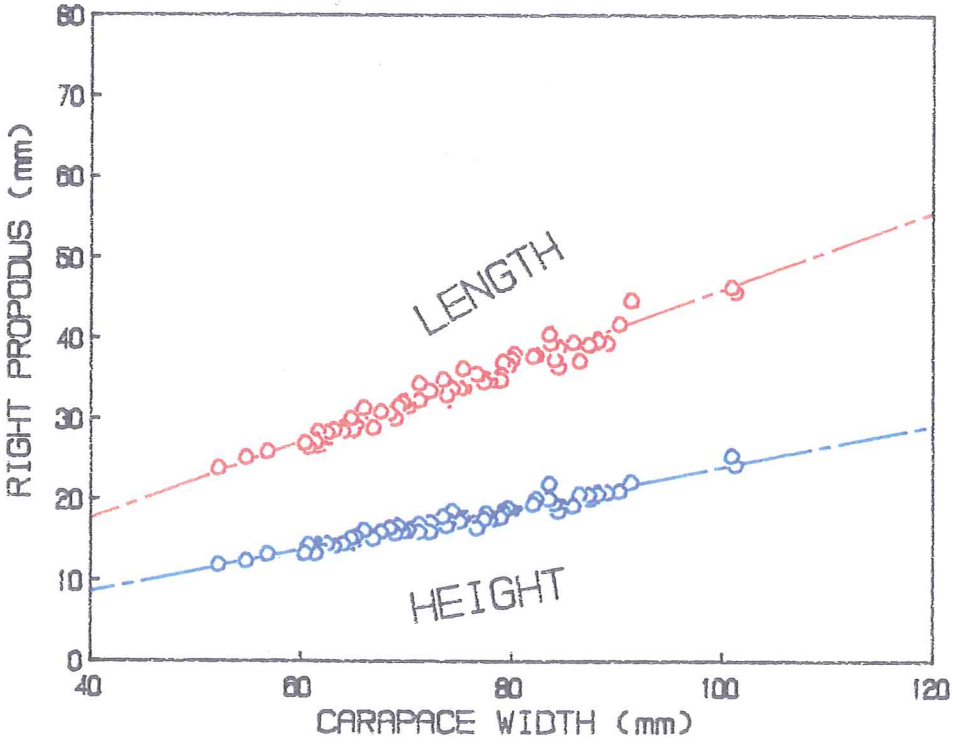

RIGHT PROPODUS (mm)
0
10
20
30
40
50
60
70
80
LENGTH
HEIGHT
40
60
80
100
120
CARAPACE WIDTH (mm)

Table 3.3. Comparison of linear constants of regression equations of propodus between male and female *C.novaezelandiae*.

	t	df	N	
Left Propodus Height				
Y-Intercept	0.015	1	245	NS
Slope	0.212	1		NS
Left Propodus Length				
Y-Intercept	0.660	1	243	NS
Slope	1.150	1		NS
Right Propodus Height				
Y-Intercept	0.950	1	236	NS
Slope	1.160	1		NS
Right Propodus Length				
Y-Intercept	0.029	1	236	NS
Slope	0.476	1		NS

increased at a faster rate than propodus length, ultimately conferring a robust, thick-bodied shape. Growth of the chelae dimensions was significantly positively allometric. Although chela growth appeared to remain constant with increasing crab size, there was a slight indication of an increase in allometry for male crabs greater than 110.0 mm carapace width.

Mechanical Properties.

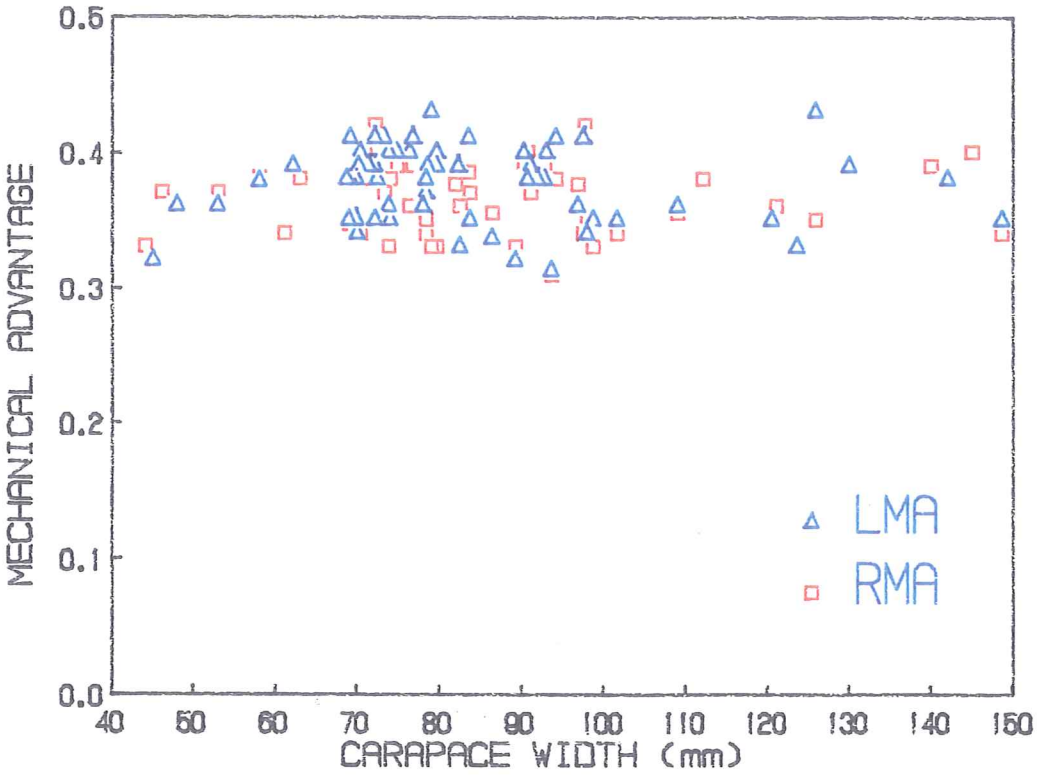
The left and right chela have a mean mechanical advantage of 0.3668 $\pm$ 0.028, n=61, 0.376 $\pm$ 0.02996, n=56, 0.3691 $\pm$ 0.201, n=23, and 0.3743 $\pm$ 0.03394, n=20 for males and females, respectively, which were not significantly different (t=1.5, df=115, NS; t=0.506, df= 41, NS). No differences were found with respect to mean MA for left and right chela of males and females (t=0.296, df=82, NS; t=0.1723, df=74, NS). The relationship of MA and crab size is shown in Fig 3.8. Regression analyses suggests that MA remains constant throughout crab growth (F=2.63, df=77; P=0.097, F=0.467, df=75, P=0.6343 for left and right chela, respectively).

Observations Of Feeding Behaviour

Food is first directed into the oral cavity using the chelae, usually in the form of relatively large food fragments. Here, the third maxillipeds initially grasp tissue, which in turn, proceed to grip and tear the food into smaller, more manageable fragments before shunting food towards the mandibles. The development of a strong crista dentata of the third maxilliped was important in dealing with large fragments of tissue. Setae present along the

Figure 3.8. Relationship between mechanical advantage and carapace width of left (n=79) and right (n=77) chela in C.novaezelandiae.

Sexes combined.


MECHANICAL ADVANTAGE
0.5
0.4
0.3
0.2
0.1
0.0
40
50
60
70
80
90
100
110
120
130
140
150
CARAPACE WIDTH (mm)
LMA
RMA

crista dentata, as well as the endopod and exopod, facilitated gripping of food during transfer to the mandibles.

Once food has passed the third maxillipeds, it is directed by the first, second and third maxillipeds and first and second maxillae towards the mandibles. Crushing and tearing of food is undertaken primary by the mandibles. Food shunted into the mandibles is finely shredded by the strong mandibular incisor edge before it is directed towards the fore-gut by the action of the mandibular palps. Apart from the third maxillipeds and mandibles the remaining mouthparts are not involved in food maceration. Instead their function is to sort and direct food fragments towards the mandibular processes.

DISCUSSION

The mouthparts, gastric mill and chelae of Cancer novaezelandiae show structures that suggest that a wide array of food types encountered, be they animal or plant, living or dead, hard or soft shelled, can be effectively manipulated, crushed and masticated both externally and internally prior to digestion.

The structure of mouthparts of C.novaezelandiae are typical of both cancrid and portunid crabs. The third maxillipeds and mandibles are the principle means of food maceration prior to ingestion and hence both are large and of generalised structure. The remaining mouthparts are not involved in food maceration; instead they act to sort and direct material towards the mandibles.

The relationship between functional mouthpart morphology and diet has gained little attention in previous studies concerning mouthpart structure. Skilleter and Anderson (1986) examined the of mouthpart morphology and diet for two species of crab, Ozius truncatus (Xanthidae) and Leptograpsus variegatus (Grapsidae). Marked morphological differences of the third maxillipeds and mandibles were found between the two species which were attributed to different activities of the mouthparts during feeding. O.truncatus is a predator of gastropod molluscs. The third maxillipeds are large in size, and bear a well developed crista dentata along the medial edge. The mandibles are large, rounded processes. The development of these mouthparts enables

gripping and tearing of large food fragments. L.variegatus, however, feeds predominantly on algal material using its chelipeds to pluck and scrape algae off rocks and stones. The third maxillipeds are reduced in size, with a less developed crista dentata comprising of 3-4 blunt teeth. The mandibles show a distinct angular process. The mouthparts of L.variegatus are well adapted to process already finely shredded food. Hence the reduction in development of the third maxillipeds and mandibles reflect their small involvement during the feeding process.

The mandibles of Ebalia tuberosa (Leucosidae) are similar to O.truncatus, but the third maxillipeds are more reduced and lack the crista dentata (Schembri, 1982). This type of mouthpart is well suited to feed on small animals and detritus which characterize the diet.

The Banana shrimp Penaeus merguiensis feeds on a wide range of food items including molluscs, crustaceans, foraminiferans and plant material. It possesses heavily setosed mouthparts, as well as enlarged mandibles (Alexander and Hindley, 1985). The endopods of the second maxillipeds and the paragnath are lined with glands opening to the surface via pores. Although the nature of these glands remains unclear, it is believed that they are responsible for digestive secretions.

The presence of a strongly developed crista dentata on the third maxilliped of C.novaezelandiae and the development of large incisor-edge mandibles appears to be a common feature among

predatory brachyurans. They are present in Carcinus maenas (Borradaile, 1922), Ovalipes guadulpensis (Caine 1974), and Scylla serrata (Williams, 1978). The crista dentata is adapted to perform two functions; to crush small fragments of shell, and to function as a clamp that facilitates tearing of flesh away from shell fragments. The mandibles are also adapted to crush and tear shell and flesh before shunting food to the fore-gut. It appears that the development of crista dentata in brachyurans is associated with a large, particulate macrophagous diet.

Previous studies have not investigated if crab size and sex affect mouthpart morphology. For C.novaezelandiae no pronounced structural differences were found with respect to size or sex of crab. Therefore, the efficiency of the mouthparts during feeding is likely to remain constant irrespective of crab size or sex. However, in very small crabs (< 30 mm carapace width) efficiency to tear and grip food material may be reduced due to small size and weaker crushing capability of the mouthparts.

An interesting feature of the present study is the presence of small, fine setation over the surfaces of all mouthparts. However, along the medial margins of both maxillipeds and maxillae long, stout bristles predominate. This type of setation has been commonly observed for many decapod species (Scott, 1958; Schaefer, 1970; Barker and Gibson, 1978). Two reasons have been suggested for the predominance of setation on mouthparts. It is thought setae may hold or bind food to the surface of the mouthparts during feeding (Warner, 1977). Alternatively, they may

have a chemosensory function in assisting the "tasting" and sorting of food fragments prior to digestion. The latter appears to be the case for the first maxilliped and second maxillae of Penaeus merguiensis (Alexander and Hindley, 1985). The dense setation of the medial edges of the mouthparts by large, stout bristles suggest that both holding of food and chemosensory reception is also likely to be a feature of C.novaezelandiae.

The morphology of the gastric mill of C.novaezelandiae shows generalized features which suggest a diverse diet. Although the third maxillipeds and mandibles have the potential for tearing food, relatively large food fragments can still enter the fore-gut. The strongly developed crushing type of gastric mill seen in C.novaezelandiae, is therefore well equipped to macerate coarse food material.

Within the gastric mill, food is torn and crushed by the action of the large, blunt dorsal tooth of the urocardiac ossicle rubbing against the larger lateral teeth of the zygocardiac ossicles. The movement of the dorsal tooth is from posterior to anterior and thus the series of events is a straining and tearing followed by a crushing and chewing action (Warner, 1977). No size or sexual differences were observed with respect to gastric mill morphology of C.novaezelandiae.

In the present study, setation within the gastric mill was restricted to small brushes directly posterior to the urocardiac

ossicle. This arrangement suggests that such setae act as "sorters" or filters within the gastric mill (Schaefer, 1970).

The morphology of the gastric mill in C.novaezelandiae is related to the large fragmented nature of ingested food. Relationships between functional morphology of the gastric mill and diet has been demonstrated only for a limited number of decapod species. Schaefer, (1970) investigated the gastric mill morphology of three species of decapods. Cyclograpsus punctatus (Grapsidae), is a general scavenger of large particulate matter, and possesses a crushing gastric mill with large lateral accessory teeth. These teeth effectively macerate the large coarse food material in the fore-gut. Diogenes brevirostris (Diogenidae) is a filter-feeder of fine material and algae. The gastric mill is of the crushing type with reticulation of the surface of the dorsal and lateral teeth. This enables the processing of fine algal material as well as coarse particulate matter. The filter-feeding shrimp Upogebia africana (Upogebiidae) possesses a "squeezing" gastric mill with the reduction of the teeth. This structure reflects the very fine algal material that constitute the diet.

The relationship between diet and gastric mill morphology has also been demonstrated for O.truncatus and L.variegatus (Skilleter and Anderson, 1986). A small number of ridges of the lateral teeth and a general robustness of the masticatory ossicles is related to the pulverization of large food particles which characterize the diet of O.truncatus. However, the delicate

nature of the gastric mill reflects the diet of L.variegatus where setation is well developed and finer toothed ossicles predominate. The degree of setation within the gastric mill has been suggested to reflect diet. Schaefer (1970) noted that the amount of setation generally increases from a diet of coarse material towards more finer aqueous matter.

In the present study, C.novaezelandiae was found to possess large blunt maceratory teeth and reduced setation in the gastric mill. These features suggest that the fore-gut is adapted to coarse particulate matter which is a result of a macrophagous diet.

As with the mouthparts and gastric mill, cheliped morphology and their mechanical properties may reflect diet. As the chelae are the principle agents for the capture and manipulation of prey, their size and structure may determine the type and size of prey which can be successfully exploited.

C.novaezelandiae is homeochelous and therefore is typical of cancrid species. The two chelipeds are morphologically similar in size and shape, and growth of the chela in male and female crabs is similar. While most cancrids exhibit homeochely, Vermeij (1976), found that from a survey of 16 species, 82% exhibited a larger right cheliped. Thus C.novaezelandiae is the exception rather than the rule. For male crabs greater than 110 mm carapace width, a small increase in chela growth rate was apparent. Similar findings have been observed by McLay (pers. comm.). This

suggests that an increase in chela size may enable large crabs to feed more efficiency by possessing larger, more stronger chelipeds. An increase in chela growth rate at large crab size has not been reported in previous studies for any brachyuran species.

Homeochely is an unusual feature amongst brachyurans, with the majority being heterochelous. For example, molluscivorous species including Ovalipes catharus (Davidson and Marsden, 1987), Ovalipes punctatus (Du Preez, 1984), Ovalipes stephensoni (Haefner Jr., 1985) and Scylla serrata (Barker and Gibson, 1978) generally have one enlarged cheliped. In the portunid crabs the "master" chela is usually larger, more robust and serves to crush prey, whilst the smaller "cutter" chela is longer, more slender and acts to hold and manipulate prey (Elner, 1980). These differences are generally less marked in female crabs where both chelae resemble cutter-like chelipeds. It has been suggested that dimorphic crabs exhibit polyfunctional chelae (Brown, Cassuto and Loos, 1979; Du Preez, 1984), each employed for different roles during predation of molluscs. Usually however, individual roles of the chela during courtship, combat and territorial displays are the most frequent explanations for cheliped dimorphism. Their individual role during feeding has generally been neglected, although it has been suggested that light, slender chelipeds are adapted to catching mobile prey (Shafer, 1954, cited in Brown, Cassuto and Loos, 1979).

Polyfunctionism of the chelae satisfactory explains the predominance of heterochely in molluscivorous brachyurans. However, in homeochelous crabs this aspect has been overlooked. In the present study C.novaezelandiae is homeochelous. In conjunction of being large and robust, the chelae when closed show a permanent diastema, which is relatively uncommon amongst large brachyuran species (McLay, pers. comm.). These morphological features suggest two roles, the ability to deliver a compressive force along the entire length of the cheliped, and the ability to hold irregular, tubular and spherical objects (which is a characteristic of molluscs) within the diastema. Therefore, despite C.novaezelandiae exhibiting homeochely, both chela perform the roles of "crusher" and "cutter" exhibited by portunid crabs, even though the degree of manipulative skill is generally reduced. Therefore, despite C.novaezelandiae being homeochelous, polyfunctionism is exhibited by both chela.

It has been demonstrated that the brachyuran cheliped functions within the parameters of a idealized lever system (Vermeij, 1976; Warner and Jones, 1976; Brown, Cassuto and Loos, 1979). In the present study, mean mechanical advantage was similar for left and right chela and remained constant during crab growth. Previous studies have found that the cheliped mechanical advantage of cancrid crabs range between 0.31 and 0.40 (Vermeij, 1976). Cancer pagurus, for example, has a mean mechanical advantage of 0.32 which does not increase with crab size (Warner and Jones, 1976). C.novaezelandiae lies in between the range described by Vermeij (1976) with a mean mechanical

advantage of 0.367 and 0.375 for left and right chela, respectively. Furthermore, no sexual differences with respect to mean mechanical advantage were observed.

Investigations of cheliped properties have suggested that mechanical advantage reflects chelae function (Vermeij, 1976; Warner and Jones, 1976). Chelae of species that exhibit heterochely possess different mechanical properties. The larger crushing claw has a greater mechanical advantage than the smaller cutter claw. This is the case for Portunidae and Xanthidae. These differences are directly related to chela function as applied stress is positively correlated with mechanical advantage. The "crusher" with a high mechanical advantage acts to crush prey. The "cutter", however, acts to hold, manipulate and slice prey, and therefore, has a much reduced mechanical advantage. This is important for catching mobile prey such as fish. For example, the strong crushing claw of Macropipus depurator (Portunidae) has a mean mechanical advantage of 0.248 $\pm$ 0.066 and is capable of exerting a force of 146.9 $\pm$ 10.3 $kN.m^{-2}$. Whilst the small fast cutting claw has a small mean mechanical advantage of 0.177 $\pm$ 0.006 and exerts a lower force of 142.9 $\pm$ 13.1 $kN.m^{-2}$ (Warner and Jones, 1976).

Homeochelous brachyurans on the otherhand, show similar mechanical properties of both chelae and therefore are expected to produce similar compressive forces during crushing. The monomorphic claws of C.pagurus have a mean mechanical advantage of 0.32 $\pm$ 0.01. This MA is capable of exerting a mean maximum

stress of 496 $kN.m^{-2}$ which is capable of being maintained over a long period of time (Warner and Jones, 1976). The large, robust chela of C.novaezelandiae are morphologically similar to C.pagurus. However, because the New Zealand species has a larger claw mechanical advantage, this suggests that it capable of exerting an even greater compressive force than 496 $kN.m^{-2}$. Such cheliped strength shown by C.novaezelandiae is no doubt an adaptation for predation on sedentary prey such as molluscs, which do not require great speed for catching, but considerable strength for crushing. For example, forces required to crush the bivalve Rangia cuneata ranged from 2 to 200 Newtons for small (10 mm) and large (90 mm shell length), respectively (Blundon and Kennedy, 1982). Compressive stress produced by C.novaezelandiae are probably well above those required to crush R.cuneata. Whereas only small clams (<40 mm) were vulnerable to crushing by large (100-165 mm carapace width) portunid Callinectes sapidus which is capable of exerting 111.2 ± 33.5 $kN.m^{-2}$.

In conclusion, it has been shown that the large, robust feeding apparatus of C.novaezelandiae has evolved morphological features which allow for the capture, manipulation, maceration and mastication of a diverse range of food types of a wide size range. Hence, the morphology of the mouthparts, chelae and gastric mill suggest a generalised macrophagous diet of prey such as sedentary molluscs, crustaceans and annelids. Furthermore, no morphological differences are observed between crabs of different size or sex. Since structural morphology is related to function, therefore, for the size range investigated dietary composition

should not vary between males and females crabs or between small, medium or large crabs.

The understanding of the influence of functional morphology on the feeding apparatus is vital if the feeding ecology for a particular species is to be fully appreciated. Numerous studies have examined diet and mouthpart, gastric mill and cheliped morphology, but emphasis was placed in treating each as a separate component. However, because they are functionally interrelated, the feeding apparatus of brachyurans should be investigated simultaneously. This has been the approach in the present study of C.novaezelandiae.

CHAPTER FOUR

PREDATORY BEHAVIOUR OF *CANCER NOVAEZELANDIAE* FEEDING ON MOLLUSCS

INTRODUCTION

It has long been recognised that many brachyurans are important predators of molluscs. These include Liocarcinus puber (ap Rheinallt and Hughes, 1985; Choy, 1986); Liocarcinus holsatus (Choy, 1986); Callinectes sapidus (Menzel & Hopkins, 1956; Krantz and Chamberlin, 1978; Blundon and Kennedy, 1982; Arnold, 1984); Carcinus maenas (Walne and Dean, 1972); Elner, 1978, 1980; Elner and Hughes, 1979; Elner and Raffaelli, 1980; Jubb, Hughes and ap Rheinallt, 1983; ap Rheinallt, 1986); Ovalipes catharus (Wear, 1984; Wear and Haddon, 1987; Davidson, 1986); Ozius truncatus (Chilton and Bull, 1986); Mercenaria mercenaria (Whetstone and Eversole, 1978); Cancer magister (Seed, 1969); Cancer antennarius (Harger, 1972); and Cancer pagurus (Boulding, 1984; Lawton and Hughes, 1985). The way predators select prey is central to our understanding of predator-prey systems. These studies have illustrated that crabs can exert an important influence on molluscs by influencing population size, structure and distribution. Furthermore, brachyuran-prey relationships may exert strong evolutionary pressures which necessitate both predator and prey to change morphologically in order to maintain co-existance (Krebs and Davies, 1981). These changes include: modifications in chela shape, dentition and strength in crabs;

and the development of spines, short spires, thickened walls, thick operculum and narrowing of the aperture in gastropods; and presence of lamellae and narrowing of gape in bivalves (Vermeij, 1976; Zipser and Vermeij, 1978; Griffiths and Seiderer, 1980; Bertness and Cunningham, 1981; Boulding, 1984). However, many of these studies pertain to portunid species, notably C.maenas, C.sapidus and L.puber, feeding on the bivalve Mytilus edulis and gastropods Littorina spp. and Nucella lapillus.

The internal structure of molluscs are characteristically protected by hard shell parts. Therefore in order to feed on soft parts, the external shell of molluscs must be broken. Many of the studies mentioned above have demonstrated that brachyurans use specific techniques to open bivalve and gastropod species. These techniques appeared to be dependent upon prey size. For example, three techniques were required by L.puber to open various size M.edulis and five to open Littorina rudis (ap Rheinallt and Hughes, 1985). Mussels were opened either by direct crushing of the shell, umbone or posterior crushing. Gastropods were opened by crushing, breakage of the aperture lip or removal of spire. Similar methods were employed by C.pagurus feeding on N.lapillus (Feare, 1970). The success of these techniques was influenced by prey size, as direct shell crushing was only successful for small prey. O.catharus employed five opening techniques to open M.edulis aoteanus (Wear, 1984; Davidson, 1986). Besides those already mentioned above, splitting of valves and chipping of the posterior shell edge were successful for large mussels, but these methods were time consuming. Similar techniques have been

observed for C.maenas (Cunningham and Hughes, 1984; Ameyaw-Akumfi and Hughes, 1987). Elner (1978) suggested that C.maenas sort prey weak spots by trial and error. Some species of crab show distinct specialization with respect to opening shells. Oxystomatous crabs (Calappinae) possess large specialized teeth on both the dactyl and propodus of the right cheliped which are associated with opening of gastropod shells, particularly when feeding on hermit crabs (Shoup, 1968). The majority of studies concerned with prey opening techniques have failed to investigate whether crab size was an important factor determining attack success for a particular opening technique. Nevertheless, most authors agree that the importance of relative strengths of prey shell and crab chela impose a limit to prey size (Williams, 1978).

Times required to open and consume various prey species have received considerable attention (Elner and Hughes, 1978; ap Rheinallt and Hughes; 1985; Chilton and Bull, 1986). Many studies have shown that handling times are dependent on both crab size and species, and size and species of prey. However, most studies use a single bivalve or gastropod species (usually similar prey types are used in all studies ie. M.edulis). Few have investigated more than one prey species.

Many studies investigating brachyuran feeding ecology have attempted to relate their findings to the Optimal Foraging Theory. The Optimal Foraging Theory has received considerable attention in the past twenty years in both marine and terrestrial ecology (Werner and Hall, 1974; Elner and Hughes, 1978; Milton,

1979; Lewis, 1980; Tinbergen, 1981; Gardner, 1981; Hughes and Seed, 1981; Mittelbach, 1981; Barnard and Stephens, 1981; Davidson, 1986). As a result, this theory has received rigorous testing and subsequently modification. The application and testing of such a model is useful as a theoretical tool giving useful insights to predator-prey systems, particularly with regard to potential stabilizing strategies (Elner and Hughes, 1978). Therefore the value of the Optimal Foraging Theory lies not in its theoretical foundations, but in its heuristic functions (Kamil and Yoerg, 1982; cited in Grey, in press). A critical review of the Optimal Foraging Theory is given by Krebs, Stephens and Sutherland (1983); Pyke (1984) and Gross (1986).

The Optimal Foraging Theory was established largely by MacArthur (1972) in which he asked "Where should an animal feed to get the most food, and what items of food should it pursue ?" Through subsequent theoretical advances originated the "Energy Maximization Premise" whereby a predator chooses its diet to maximize the net energy intake per unit foraging time (Elner and Hughes, 1978). This theory assumes that predators are capable of visually identifying and ranking prey items based on their energetic value (ie "Prey Profitability"). Hughes (1978) restated the theory to include non-visual predators with finite prey recognition times, probability of prey misidentification and the effect of learning by the predator. This is defined by the inequality :

$$\frac{1}{v_1} < \frac{E_1 Th_2}{E_2} - (Th_1 + Tr_1) - \frac{v_2}{v_1} \cdot Tr_2$$

where :

v_i = rate of encounter.

E_i = energy yield.

Th_i = handling time.

Tr_i = prey recognition time.

However in the following experiments, rate of encounter, prey recognition time and search time were held constant and so if presented with two prey species or sizes the following inequality can be applied.

$$P_a > P_b = \frac{E_a}{Th_a} > \frac{E_b}{Th_b}$$

where :

P_i = prey species or size.

E_i = energy yield.

Th_i = handling time.

Such that if given a choice of prey species or size, crabs should select prey of highest profitability (ie. in this example, $Prey_a$ should be preferred over $Prey_b$). This is the Energy Maximization Premise".

In most marine studies, optimal foraging has been investigated using the Energy Maximization Premise. However, not all have found the theory to be applicable for all crab and prey species. It has been demonstrated for C.maenas that when presented with a range of M.edulis, male crabs selected mussel size with the highest profitability (Elner and Hughes, 1978). Similar results have been demonstrated for C.sapidus (Hamilton, 1976), L.puber (ap Rheinallt and Hughes, 1985) and O.truncatus (Chilton and Bull, 1986). However, many other crab species tend not to select optimum prey, but rather choose smaller, sub-optimal size or species. This has been demonstrated for C.pagurus (Lawton and Hughes, 1985), O.catharus (Davidson, 1986) O.punctatus (Du Preez, 1984), Scylla serrata (Hill, 1979a). Hughes and Seed (1981) suggested that crabs were faced with a "trade off" between maximizing energy gained, and minimizing time spent foraging. This trade off may explain why crabs may fail to select optimum prey size when presented with a choice.

Few studies have examined prey species selection with respect to the Energy Maximization Premise. The lack of information regarding whether crabs select prey species based on their energetic value is a serious omission, particularly in the current light of the Optimal Foraging Theory dilemma. Prey species differ in profitability due to differences in both prey energetic value and handling time. Therefore a valuable test of the Energy Maximization Premise is to investigate whether crabs select prey species of a given size when presented with a choice

of species of different profitability. Sadly, however, a paucity of information exists regarding prey species selection.

The deficiency in the number of brachyuran and prey species examined leads to simple generalizations regarding crab/prey feeding ecology. Such generalizations do not consider the influence of crab species, size and sex, and prey species, size, shell morphology, profitability, vulnerability and anti-predatory adaptations. Moreover, few studies have examined predator-prey relationships with respect to cancrid crabs. Therefore it would be of particular interest to make comparisons between portunid and cancrid crabs as they are morphologically, physiologically and behaviourally different (Warner and Jones, 1976; Vermeij, 1976; Lawton and Hughes, 1985).

This chapter is concerned with investigating the effect of prey species and size on the feeding ecology of Cancer novaezelandiae. Laboratory experiments were undertaken using three size classes of crabs feeding on four species of molluscan prey. Molluscs were considered the most appropriate choice as prey as mollusc material was found to dominate the natural diet (see Chapter Two). Prey used included bivalves Mytilus edulis aoteanus and Chione stutchburyi and gastropods Cominella maculosa and Turbo smaragdus. These species are known to occur in the habitat where C.novaezelandiae was collected (pers. obs.). All four species are different in geometric shape, anti-predatory adaptations and energetic value. Experiments were designed to investigate, opening techniques used and how these were

influenced by crab size, chela morphology, and prey size and shell morphology; influence of crab size on critical upper and lower prey size; handling time and the influence of crab size, and prey size and shell morphology; prey profitability; consumption rates and the influence of crab size; and the extent to which C.novaezelandiae exhibits prey size and species selectivity, and to place these findings into the context of the Energy Maximization Premise.

METHODS AND MATERIALS

Cancer novaezelandiae were collected from Diamond Harbour, Lyttelton between June 1985 and October 1987. All collections were made using baited traps lowered to a range of depths between 0.5 and 5.5 m (see Chapter Two). Once collected, crabs were transported to the laboratory and within three hours were held in a recirculatory seawater system at 16-18 ^{o}C and under fluorescent lights on a 12 light / 12 dark regime at a salinity of approximately 36 ppt. Only male crabs were used in all experiments to reduce variability caused by possible sexual differences in morphology and predatory behaviour. Crabs with lost or regenerated chelipeds or walking legs were not used.

Four prey species were used for laboratory work (Plate 4). Prey used were blue mussel Mytilus edulis aoteanus, collected from the upper mid-tidal zone of North Brighton beach, Christchurch (43^{o} 29'S, 172^{o} 43'E); cockle Chione stutchburyi, collected from the low inter-tidal zone of Avon-Heathcote Estuary, Christchurch (43^{o} 33'S, 172^{o} 44'E); spotted whelk Cominella maculosa and catseye Turbo smaragdus, both collected from mid-tidal levels of Lab Rocks and Wairepo Flats, Kaikoura (42^{o} 25'S, 173^{o} 42'E). In order to ensure prey freshness and consistency, collections were made regularly and only undamaged individuals in good condition were used as prey items.

Crab size was determined by measuring carapace width as described in Chapter Three. Prey size was measured using Vernier

Plate 4. Prey species presented to *C. novaezelandiae* in the laboratory. Blue mussel *Mytilus edulis aoteanus* (top left), cockle *Chione stutchburyi* (bottom left), spotted whelk *Cominella maculosa* (top right) and catseye *Turbo smaragdus* (bottom right).

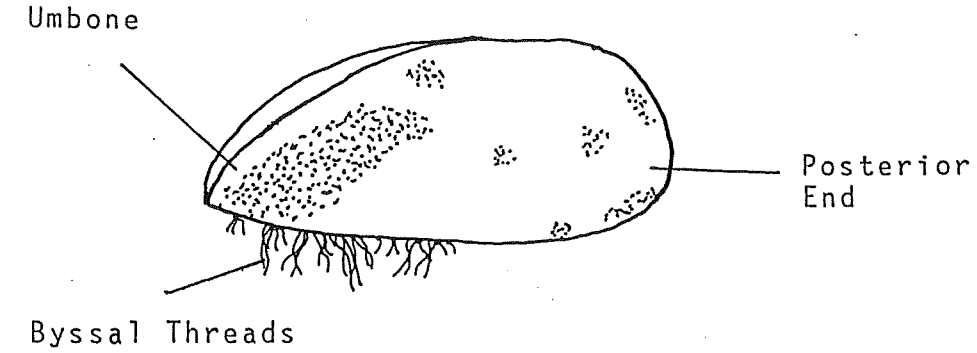
calipers to the nearest 0.1 mm. Bivalve length was measured along the longest axis of the shell. Gastropod height was measured from spire tip to posterior tip of the siphonal canal (Figure 4.1).

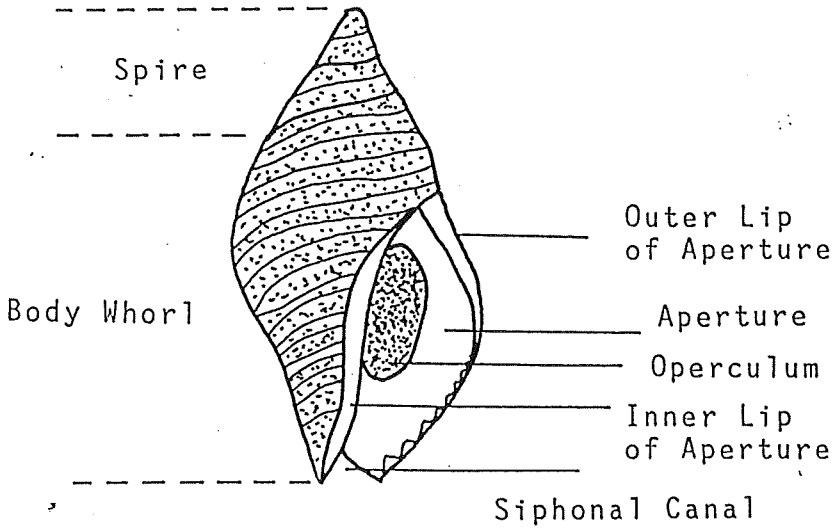
Four main series of experiments were performed. The first series, involving all four prey species, was designed to investigate handling techniques employed to open prey. The second series was designed to measure handling times, and upper and lower critical prey size and involved all four prey species. The third series was designed to investigate prey-size selection of mussels and whelks. These experiments also allowed determination of consumption rates for crabs of different size. The fourth series involved choice experiments between mussels and cockles. The first, second and third series of experiments used three size categories of crab, small 55.0-65.0, medium 80.0-90.0 and large 105.0-115.0 mm carapace width. The fourth series of experiments used large crabs only. At the beginning of all experiments crabs were starved for 24 hours in order to standardize hunger level. This length of time was considered adequate, as starvation periods longer than one day (which tends to be the case for many studies) may create erroneous feeding rates due to crabs subjected to unnatural starvation levels.

Opening Techniques

Four large, medium and small crabs maintained individually in large glass aquaria (36x20x38 cm) were randomly presented with individual prey of a particular species, over a wide size range. Behavioural responses to prey and details of each attack sequence

Figure 4.1. Shell morphological features. Bivalve (*Mytilus edulis aoteanus*, top), and gastropod (*Cominella maculosa*, bottom).


Umbone
Posterior End
Byssal Threads


Spire
Outer Lip of Aperture
Body Whorl
Aperture
Operculum
Inner Lip of Aperture
Siphonal Canal

made by each crab were continuously observed and recorded. Shell fragments were collected after successful attacks to aid in interpretation of the observed breaking technique. The cheliped used to open prey (left or right) was also noted. Once prey had been opened, consumed or rejected another of a different size was immediately presented and the above procedure repeated. The success or failure of each attack was recorded enabling critical upper and lower prey size to be established. For each crab size class, approximately 60 trials were performed for each prey species. Different crab individuals were used during all experiments. All trials were performed under natural daylight conditions.

Handling Times

During experiments investigating opening techniques of crabs presented with individual prey, the following events were also recorded with the aid of a stopwatch:

i] Breaking Time (Tb). Tb was defined as the time from the crab's first attempt to open prey, through the period of recognition and shell crushing, to the first bite of exposed flesh.

ii] Eating Time (Te). Te was defined as the period from the end of Tb to the completion of the meal and abandonment of the empty shell. Te included time spent handling and re-breaking the shell to extract all flesh.

iii] Handling Time (Th). Th was defined as the sum of Tb and Te.

This method of investigating handling times was consistent with previous studies (Elner and Hughes, 1978; Jubb, Hughes and ap Rheinallt, 1983; Lawton and Hughes, 1985; ap Rheinallt, 1986; Davidson, 1986).

Prey Profitability Determination

The relationship between energetic value and prey size was determined for cockles, whelks and catseyes by estimating yield of flesh and energetic content. Thirty freshly collected individuals of each species were measured, crushed, weighed and living tissue dried at 60^{o}C for 48 hours and reweighed. Hard parts including shell and operculum were not included in dry weight determination. This process enabled a regression equation relating dry flesh weight (g) to prey size (shell height or length) to be calculated.

The energetic content (Kj/g) of cockle, whelk and catseye flesh was measured in a Parr 1411 Bomb Calorimeter for 10 individuals of each prey species. The technique used is described by Stephenson (1981). Together, both processes enabled a determination of prey energetic content (E) on shell length or height.

The regression equation of prey energy content for M.edulis aoteanus given by Davidson (1984) was used for determination of

mussel energy content, as mussels in the present study were collected from the same area.

Prey value was defined as energetic content per unit handling time (E/Th). Profitability curves for each size and species were estimated by dividing energetic content for a given prey size by the appropriate handling time. These definitions ignore any differences in the metabolic costs of the various handling activities (Elner and Hughes, 1978).

Prey-Size Selection

Prey-size selection was investigated by presenting crabs with a fixed number of different sized mussels and whelks placed haphazardly over the aquarium bottom. Individual large (n=6), medium (n=6) and small crabs (n=6) placed in perspex aquaria (60x37x22 cm) were offered mussels of five size classes; 5-15, 20-30, 35-45, 50-60 and 65-75 mm shell length. Within each size class eight prey items were given. The numbers in each size class were maintained by replacing injured as well as eaten prey each day. Experiments were run over five days.

A similar experiment was performed using C.maculosa as prey. Large, medium and small crabs (n=4) were offered four size classes of whelks; 5-15, 16-25, 26-35 and 36-45 mm shell height. Within each size class, four prey items were presented. Initial trials indicated that whelks tended to climb the walls of the aquaria and thereby, became inaccessible. As experiments were designed to investigate size-selection only, whelks were

therefore immobilized prior to experiments. This was undertaken by immersing whelks into freshwater at 40°C for 15 minutes and then immediately subjecting them to ambient seawater for 10 minutes. A similar procedure was adopted by Lawton and Hughes (1985).

Prey-Species Selection

Four large crabs were presented with 10 mussels and 10 cockles of three size classes; 10-15, 28-35 and 40-45 mm shell length placed haphazardly over the aquarium bottom. All prey that had been eaten or injured were replaced daily to maintain equal numbers. Experiments were run over five days.

Statistical Analysis

Chi square tests using frequency data were used to test whether observed data were statistically different from expected values for investigating opening techniques versus crab and prey size, left and right handedness, and prey-size and prey-species selection experiments using 5% level of significance (H_0: no difference). Analysis of variance (ANOVA) was used for comparisons of consumption rate and crab size. All tests were performed using the statistical package STATISTIX.

Breaking, eating and handling times, and dry vs wet weight data for all four prey species were transformed using natural logarithms and regression lines were calculated using Least Squares Regression (Model I) procedure. To investigate whether regression lines and profitability curves were statistically

different, analysis of covariance (ANCOVA) were performed on all lines using statistical package BMDP-1V available on the University of Canterbury Burroughs computer. To comply with ANCOVA assumptions of parallelism of slopes all lines were transformed using Log_{10}.

RESULTS

Pre-Opening Observations

In the aquarium, large, medium and small C.novaezelandiae readily accepted individual M.edulis aoteanus, C.stutchburyi, C.maculosa and T.smaragdus. Shortly after the introduction of individual prey into the tank (approximately 5-120 seconds), an olfactory response to the prey was recognised by an increase in antennular flickering rate. Thus initial stimuli to prey appeared to be chemosensory rather than visual.

Once prey had been "sensed", the crab quickly moved in the direction of the prey which was located by rapid lateral extensions of both chelipeds. Following contact, if prey was large (mussels > 35 mm, whelks > 25 mm, catseyes > 20 mm) it was immediately swept under the body and held by the first, second and third pairs of walking legs for a period of 5-10 minutes. This procedure was undertaken before any attempts were made to open prey. This behaviour may be associated with prey recognition. If prey was small, however, it was immediately grasped and crushed by the chela or pushed into the mouthparts and readily devoured. Cockles, however, regardless of size, were accepted more quickly as attempts to open the shell began immediately after acquisition.

Following capture of small prey, attempts to open the shell usually began immediately. Large prey, however, were manipulated extensively using both chelipeds, first and second pairs of

walking legs and third maxillipeds before any attempts to open prey were made. This process involved rotation of prey using the chelipeds such that all regions of the shell came into contact with the chelipeds, mouthparts and walking legs. This manipulatory behaviour may allow the crab to "detect" prey species and size, and to assess the feasibility of opening prey and therefore whether to accept or reject prey.

Techniques Employed To Open Prey

Once prey had been accepted, attempts to open the shell immediately followed. Techniques used to open prey are described separately below for mussels, cockles, whelks and catseyes. (NB. C.novaezelandiae is homeochelous and terms "crushing" and "non-crushing" chela do not refer to one particular cheliped).

Mytilus edulis aoteanus

Five distinct techniques were employed to open mussels. These were :

1] *Direct Crushing*

Direct crushing was usually the first technique employed regardless of prey size. However, direct crushing was only successful on small mussels (< 45 mm shell length). Prey were manipulated so that the left, right or both chela enclosed the shell with the plane of the hinge line randomly orientated to the lateral crushing action of the chela. Often the umbone tip or posterior edge of the mussel was held between the third maxillipeds to provide increased leverage to the crushing chela,

as small mussels could shoot out of the chelal grip as force was applied. Mussels opened by this technique were usually highly fragmented (Plate 5).

2] *Umbone Crushing*

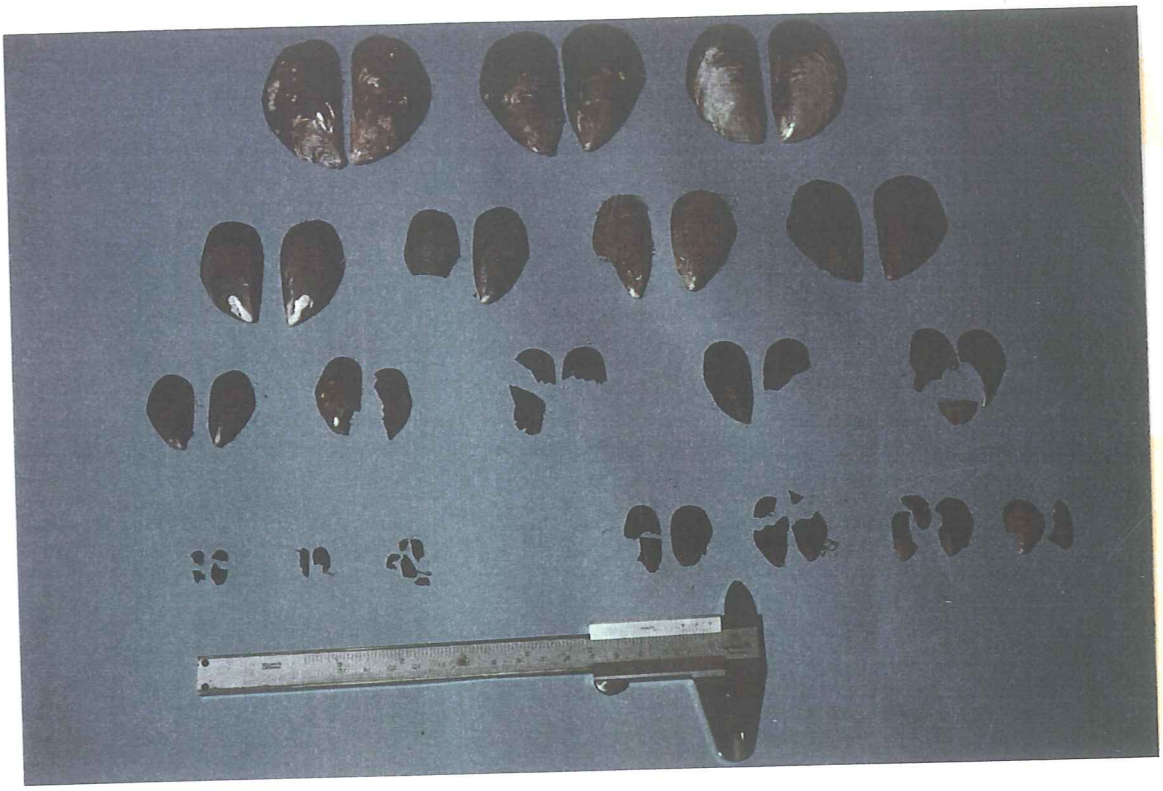
Umbone crushing was employed for mussels of all sizes, but was only successful for those of medium size (20-60 mm shell length). The shell was manipulated so that the crushing chela applied pressure directly to the umbone region with the hinge line perpendicular to the lateral crushing angle of the chela. Usually the non-crushing chela gripped the shell to steady the mussel and to increase leverage to the crushing chela.

3] *Umbone Splitting*

Splitting of the umbone involved the separation of mussel valves down the hinge line (also known as "wedging"; Davidson, 1984). This technique was employed only after direct and umbone crushing had failed. Umbone splitting was successful in opening large mussels up to 75 mm shell length. The mussel was manipulated so that the propodus and dactylus of the crushing chela lay directly in plane with the hinge line at the umbone end. Force was then applied causing the tips of the fingers to be inserted in between the shell valves. This technique resulted in prising apart of the mussel valves. Once a gap was created between the valves, the propodus and dactylus was inserted which subsequently severed the shell abductor muscle. Shell valves opened by umbone splitting were usually left intact.

Plate 5. Remains of Mytilus edulis aoteanus shells after being opened by small, medium and large crabs.

Plate 6. Remains of Cominella maculosa shells after being opened by small, medium and large crabs.




0 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160

4] *Posterior Crushing*

Crushing of the posterior region was the most infrequent method used to open mussels. This is because the shell tended to slip away from the chela due to the shape of the mussel. Only medium size mussels (20-30 mm shell length) were opened by this technique. The crushing chela enclosed the posterior region of the shell with the hinge line perpendicular to the lateral crushing action of the chela. Due to shell shape such a method usually required considerable force to fracture the shell.

5] *Posterior Chipping*

Chipping away shell of the posterior shell edge was used as a last resort after all other methods had failed. This is because posterior chipping was a very time consuming technique, and hence this method was only employed on medium and large mussels (32-75 mm shell length). The shell was manipulated such that the tips of both propodus and dactylus could be employed to chip away small fragments of shell edge. Eventually, continued chipping led to creation of gaps in between shell valves. The tip of one finger was then inserted into the gaps and shell valves were prised apart in much the same way as umbone splitting.

<u>Chione stutchburyi</u>

Four techniques employed to open cockles were observed. These were :

1] *Direct Crushing*

Direct crushing was usually employed to open small cockles

less than 30 mm shell length. Cockles were crushed in a similar way to that described for mussels. However, unlike mussels, small cockles did not tend to slip away from the chela under force. This was probably attributable to the spherical geometry of the cockle. Cockles opened by this technique were highly fragmented.

2] *Umbone Crushing*

Crushing of the umbone region was employed for cockles of all sizes. However, this technique was only successful for those of medium size (15-40 mm shell length). The umbone region was crushed in much the same way as that described for mussels. This included the assistance of the non-crushing chela, as well as the third maxillipeds which gripped the cockle to increase leverage applied by the crushing chela.

3] *Umbone Splitting*

Splitting the umbone involved the separation of the cockle valves down the hinge line in much the same way as that described for mussels. This technique was employed only after direct and umbone crushing had failed and was only successful on cockles up to 50 mm shell length. Cockle valves prised open by this technique were usually left intact.

4] *Posterior Chipping*

Chipping away shell of the posterior region was used as a last resort after all other methods had failed. This is because this method was a time consuming process. Posterior chipping was only employed on small to medium cockles (15-35 mm shell length).

Chipping of the shell edge for cockles was undertaken in a similar way for that described for mussels.

Cominella maculosa

Three distinct techniques employed to open whelks were recognisable. These were :

1] *Direct Crushing*

Direct crushing was usually employed initially to open whelks of all sizes; however, it was only successful on small whelks (< 20 mm shell height). Crabs would grasp the whelk using either chela and/or third maxillipeds, whilst the other chela was used to crush the whelk directly across the base of the body whorl. Whelks opened by this technique were highly fragmented (Plate 6).

2] *Apertural Breakage*

Opening shells by breakage of the aperture was the most common technique employed. Apertural breakage was the most successful method used to open whelks which could not to be directly crushed. Two variations of this method were evident :

i) The dactyl of one chela firmly grasped the outer lip, while the other chela tightly gripped the columella. The former was then twisted, fragmenting the lip piece by piece. This process resulted in a "peeling" of the aperture lip.

ii) The dactyl of both chela were inserted into the aperture such that the outer lip was grasped firmly by both chelae. The

chelae were then twisted in a synchronised fashion such that the force generated from one chela directly acted against the other. Such an action caused the aperture lip to fracture.

After the aperture lip had been peeled to the point of maximum operculum retraction, the columella was attacked and the flesh was removed. For larger prey sizes the combination of the operculum and shell robustness prevented further crab attack and the prey was subsequently rejected. This rejection usually allowed the damaged whelk to escape.

3] *Spire Removal*

Crabs occasionally grasped the columella with one chela, whilst the other attempted to sever the shell spire. This technique was rarely successful as the shell in this region is robust and the chela tended to slip over the apical shell whorls. Large whelks (36-45 mm shell height) were successfully opened by this technique.

<u>Turbo smaragdus</u>

Three techniques of attack were recognisable :

1] *Direct Crushing*

Direct crushing was the first technique employed regardless of prey size. No particular region of the shell was preferentially chosen as the point of crushing. This method was only successful on small catseyes (< 25 mm shell height). Shells opened by this technique were highly fragmented.

2] *Apertural Breakage*

Apertural breakage involved the removal of the lip surrounding the operculum. This technique was applied immediately after attempts to directly crush the shell had failed and was applied to catseyes between 15 and 35 mm shell height. Two variations of this technique were observed, closely resembling those observed for C.maculosa. Once the aperture lip had been peeled away, the operculum was removed before flesh could be extracted. This process involved either the severing the operculum by cutting the operculum retractor muscle, or by gouging out the operculum using the tips of the chelae. Crabs were usually successful in removing the apertural lip of large prey. However, obtaining flesh was often inhibited by the failure to remove the large, thick operculum. This resulted in the snail being rejected.

3] *Drilling*

Entry by drilling was only observed once for a 32.7 mm catseye. Drilling involved gripping of the body whorl by one chela, while the other scraped the region directly opposite the aperture. This process created a small hole in the shell wall. The tip of the propodus was then inserted into the hole and twisted, causing the hole to be increased in size. Flesh was then slowly extracted through the hole.

Once feeding had been completed small gastropods were usually entirely consumed. However, large snails were often left

half-eaten, usually with the spire intact. This may be explained by the inability of crabs to penetrate the spiral region of the whelk. However, when feeding on bivalves, all flesh was gleaned from the shell regardless of prey size.

During attempts to open all four prey species, crabs were regularly observed to manipulate the shell in order to swap over and use the other, more "fresher" chela for crushing after considerable effort had been applied by one cheliped. Furthermore, no one chela was favoured for opening shells (X^2=0.272, 0.0204 and 0.1053, df=1, NS, n=40, 60 and 38 for small, medium and large crabs, respectively).

Influence Of Crab And Prey Size On Opening Techniques

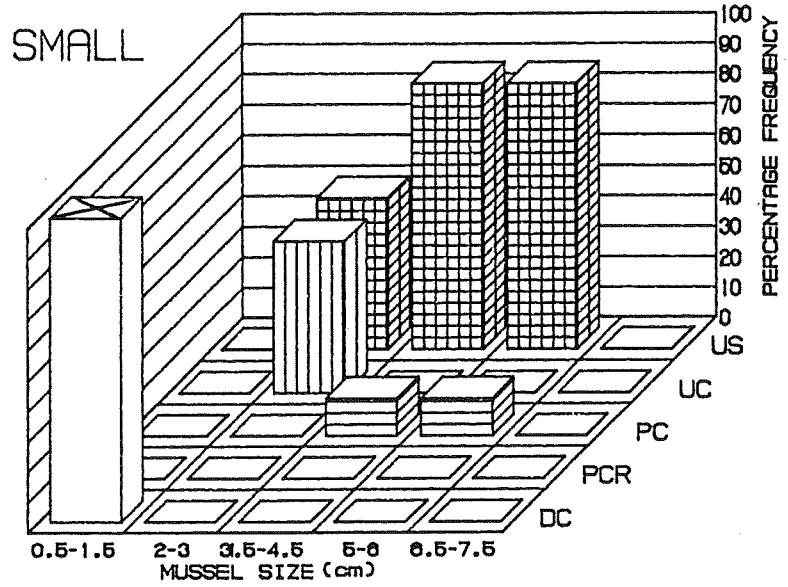
The relative frequency of opening techniques used by small, medium and large crabs to open a size range of all four prey species is shown in Figures 4.2, 4.3, 4.4 & 4.5. Goodness of fit tests showing the influence of prey size and crab size on opening technique are shown in Tables 4.1 & 4.2.

Techniques employed to open cockles and whelks were significantly influenced by crab size. For example, a wider size range of prey was enabled to be directly crushed by large crabs in comparison to smaller crab sizes. However, when mussels and catseyes were presented similar methods were used to open shells regardless of crab size.

Figure 4.2. Techniques employed to open Mytilus edulis aoteanus and prey size by small (top), medium (centre) and large (bottom) crabs.

KEY

DC = Direct Crushing.
PC = Posterior Chipping.
PCR = Posterior Crushing.
UC = Umbone Crushing.
US = Umbone Splitting.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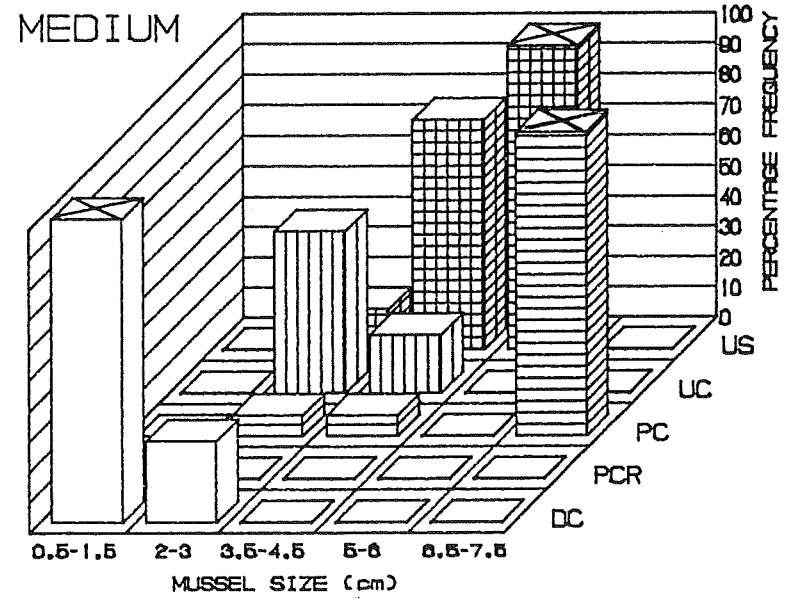
MUSSEL SIZE (cm)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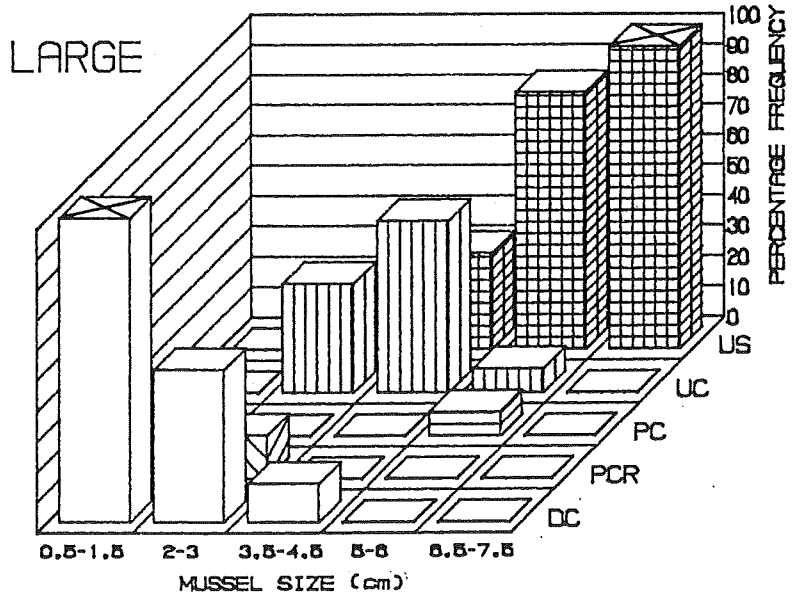
MUSSEL SIZE (cm)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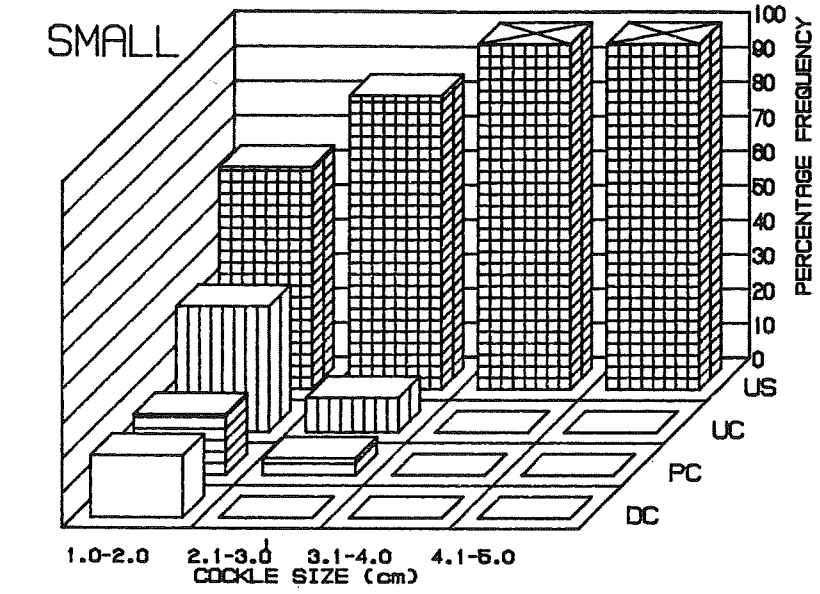
MUSSEL SIZE (cm)

Figure 4.3. Techniques employed to open Chione stutchburyi and prey size by small (top), medium (centre) anf large (bottom) crabs.

KEY

DC = Direct Crushing.
PC = Posterior Chipping.
UC = Umbone Crushing.
US = Umbone Splitting.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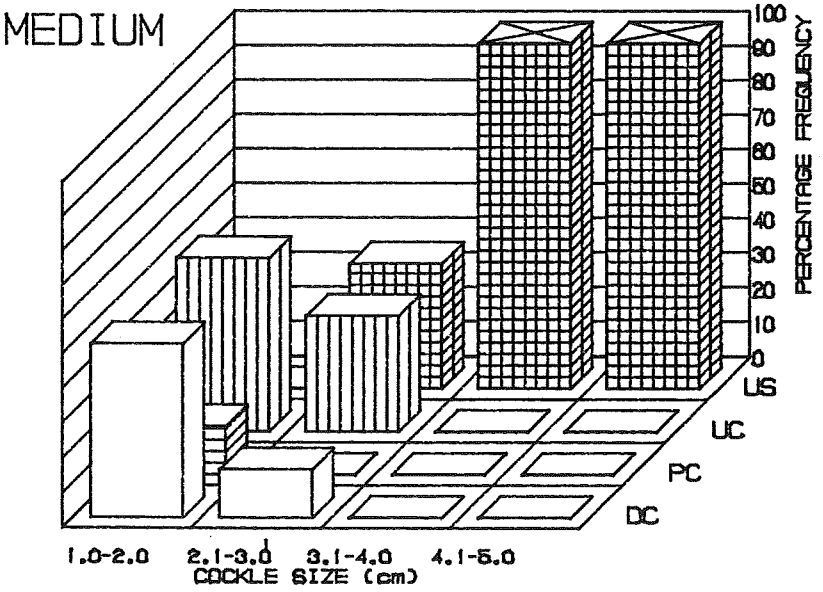
4.1-5.0
COCKLE SIZE (cm)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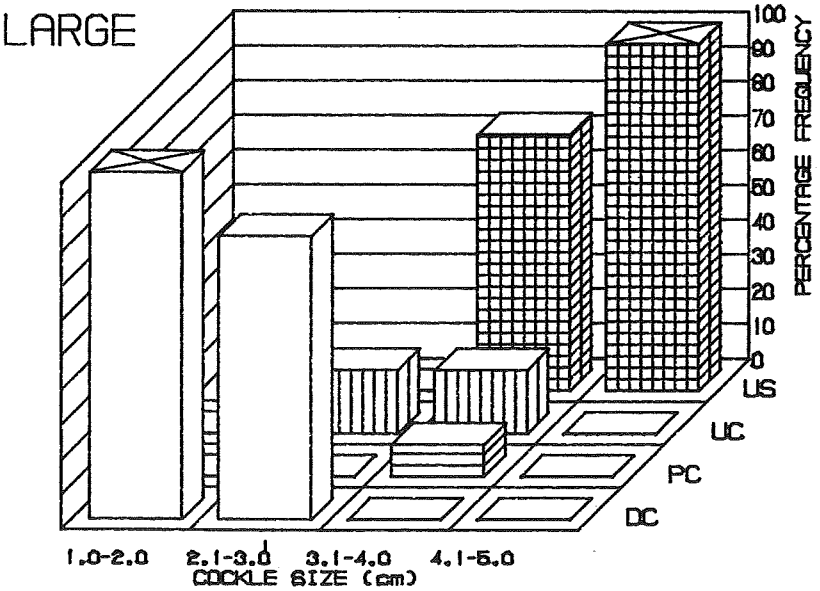
COCKLE SIZE (cm)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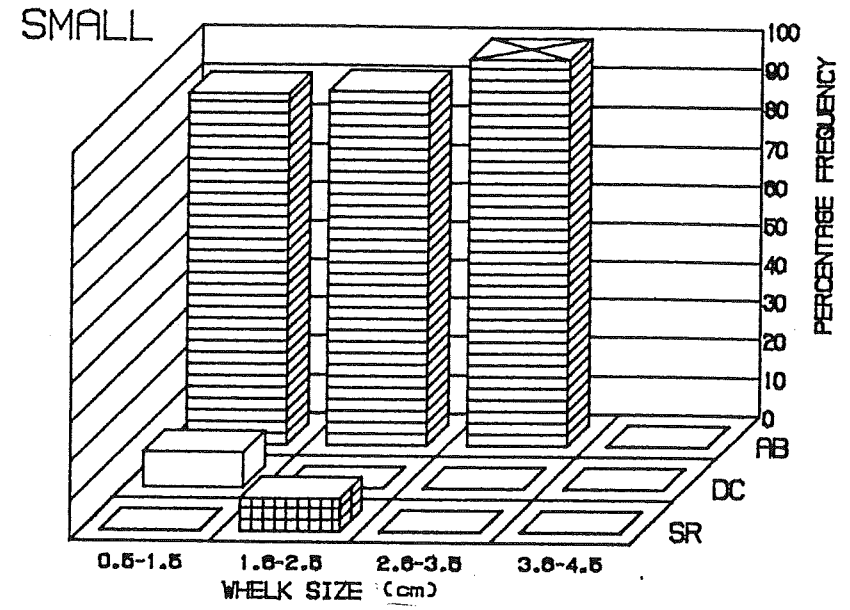
4.1-5.0
COCKLE SIZE (cm)

Figure 4.4. Techniques employed to open Cominella maculosa and prey size by small (top), medium (centre) and large (bottom) crabs.

KEY

AB = Apertural Breakage.
DC = Direct Crushing.
SR = Spire Removal.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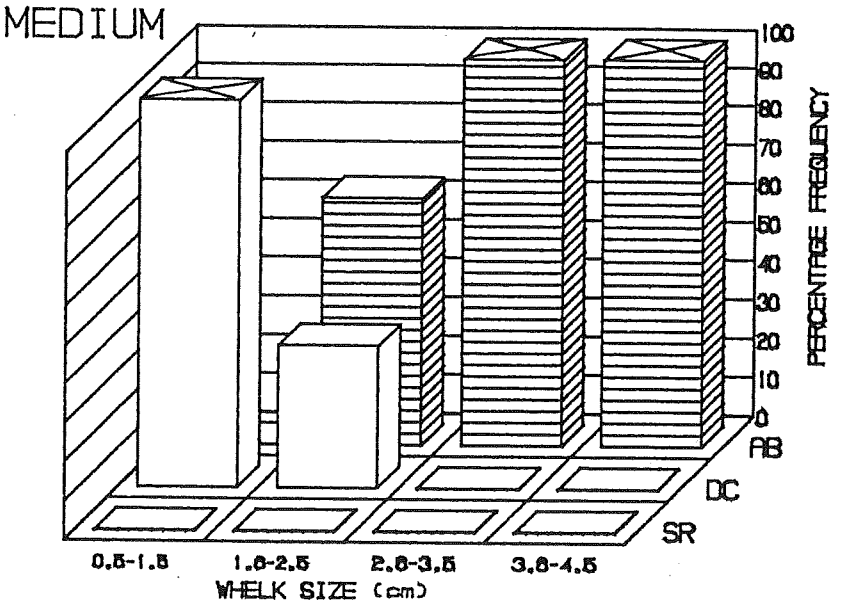
WHELK SIZE (cm)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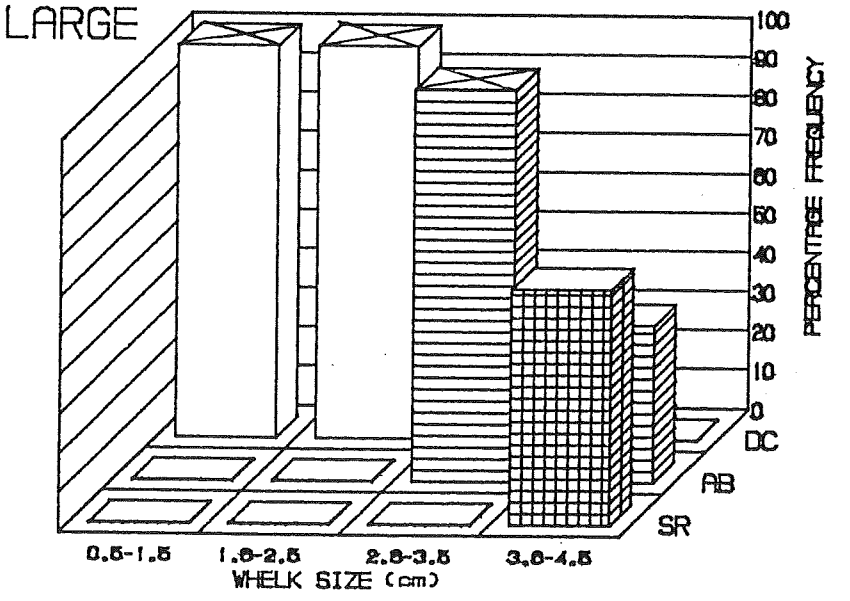
3.6-4.5
WHELK SIZE (cm)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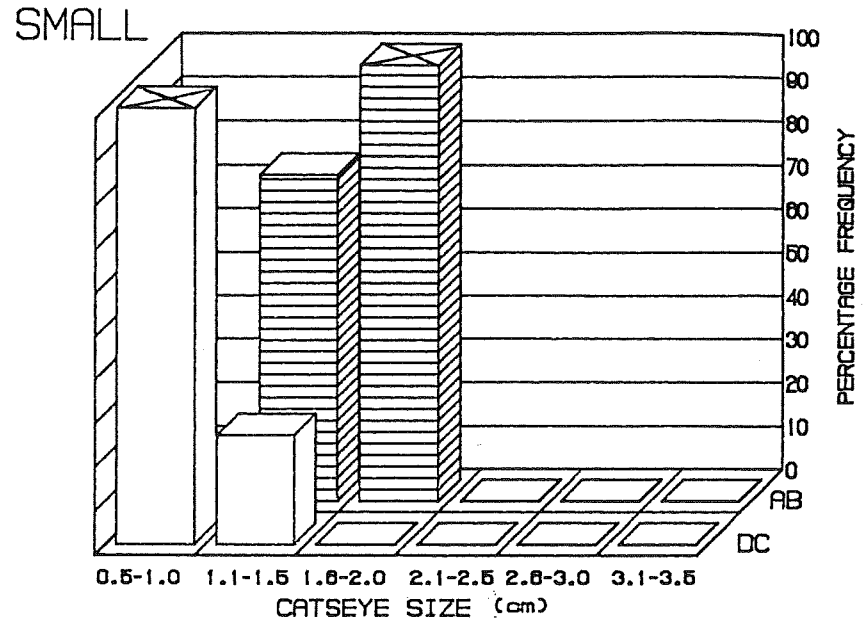
2.6-3.5
3.6-4.5
WHELK SIZE (cm)

Figure 4.5. Techniques employed to open Turbo smaragdus and prey size by small (top), medium (centre) and large (bottom) crabs.

KEY

AB = Apertural Breakage.
DC = Direct Crushing.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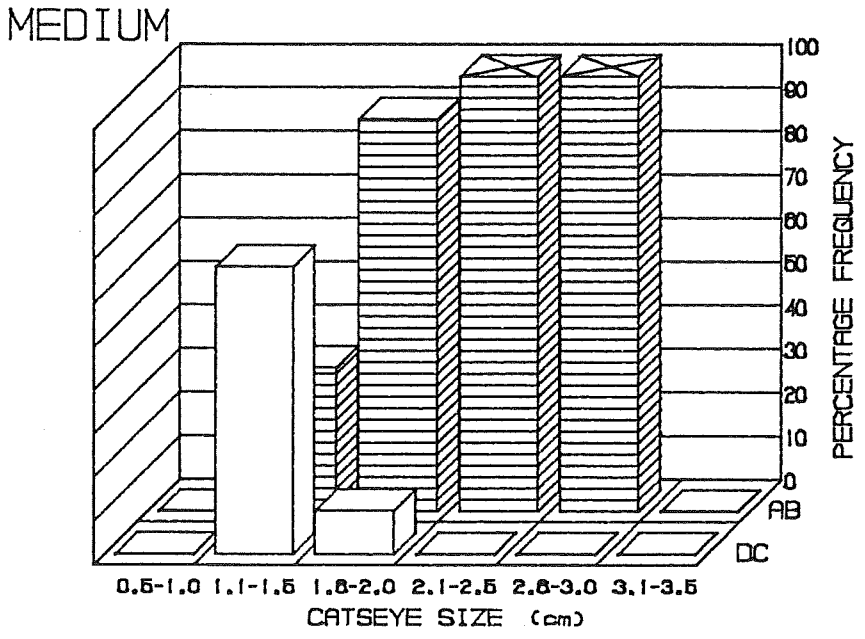
CATSEYE SIZE (cm)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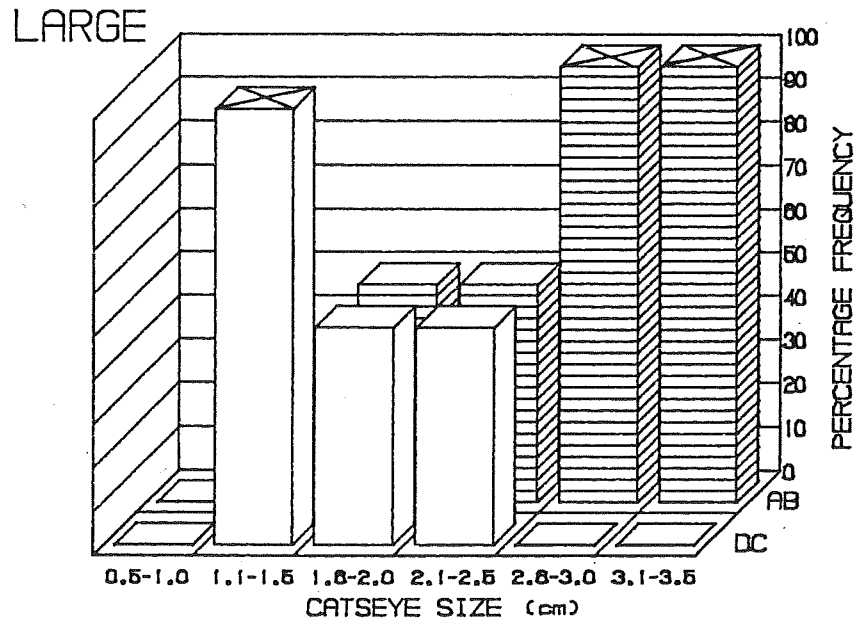
CATSEYE SIZE (cm)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CATSEYE SIZE (cm)

Table 4.1. Goodness of Fit statistics of techniques employed to open prey and prey size for large (105-115 mm carapace width), medium (80-90 mm) and small (55-65 mm) crabs.

PREY SPECIES	CRAB SIZE (mm)	X^2	DF	P	
Mytilus edulis aoteanus	Large	66.00	12	0.001	***
	Medium	85.36	12	0.001	***
	Small	73.67	9	0.001	***
Chione stutchburyi	Large	61.92	9	0.001	***
	Medium	30.80	9	0.001	***
	Small	11.37	9	0.498	NS
Cominella maculosa	Large	31.31	6	0.001	***
	Medium	23.02	3	0.001	***
	Small	2.91	4	0.276	NS
Turbo smaragdus	Large	11.92	4	0.010	***
	Medium	8.69	3	0.033	**
	Small	8.00	2	0.018	**

Table 4.2. Goodness of Fit statistics of techniques employed to open prey and crab size. (Crab size classes grouped).

PREY SPECIES	X^2	DF	P	
Mytilus edulis aoteanus	5.49	6	0.482	NS
Chione stutchburyi	62.18	6	0.001	***
Cominella maculosa	15.48	4	0.004	***
Turbo smaragdus	1.98	2	0.372	NS

When individuals of all four prey species were presented to large and medium crabs, opening techniques were significantly influenced by prey size. For small crabs, prey size was only important when presented with mussels and catseyes. Hence as prey size increased, different techniques were progressively employed depending on previous success of a particular method. For example, when individual mussels were presented to large crabs, the order of techniques employed were: direct crushing, umbone crushing/posterior crushing/posterior chipping, umbone splitting. However prey size was not a significant factor when small crabs were presented with cockles and whelks. Instead small crabs employed one technique regardless of prey size. For example, umbone splitting and apertual breakage were the principle methods used to open cockles and whelks respectively.

Critical Prey Size

Critical upper and lower prey sizes which could be successfully opened are shown in Table 4.3. Maximum prey size increased with increasing crab size for all four prey species. Minimum size of successful prey attack decreased with decreasing crab size for mussel, whelk and catseye prey but not for cockles.

Handling Times

Regression analyses relating handling time components to crab size, and prey size and species are shown in Tables 4.4, 4.5 & 4.6, and Figure 4.6. Handling time components of successful attacks for a particular prey species appeared to be exponential functions of prey size. Time required to open the shell and

Table 4.3. Critical maximum and minimum prey size for large (105-115 mm carapace width), medium (80-90 mm) and small (55-65 mm) crabs.

PREY SPECIES	CRAB SIZE	MINIMUM (mm)	MAXIMUM (mm)
Mytilus edulis aoteanus	Large	11.0	72.0
	Medium	10.0	70.4
	Small	9.0	56.7
Chione stutchburyi	Large	6.5	44.3
	Medium	10.5	40.7
	Small	13.4	39.0
Cominella maculosa	Large	12.2	40.7
	Medium	11.4	40.0
	Small	10.5	28.0
Turbo smaragdus	Large	12.1	36.5
	Medium	11.2	32.7
	Small	7.2	18.9

Table 4.4. Summary of regression analyses for breaking, eating and handling time and prey species for large (105-115 mm carapace width) *C.novaezelandiae*. All lines transformed using natural logarithms.

Prey : MU = mussel, CO = cockle,
WH = whelk, CA = catseye

a = Y-Intercept, b = Slope,
SE_b = Standard Error of the Slope,
F = Regression Significance, n = Sample Size,
r^2 =Correlation Coefficient.

BREAKING TIME (Tb)

Prey	a	b	SE_b	F	n	r^2
MU	-2.4453	2.2367	0.1391	258.5	68	0.7966
CO	-9.2266	4.3903	0.3755	136.7	72	0.6700
WH	-6.8677	4.1399	0.3786	119.6	22	0.8567
CA	-4.5071	3.5071	0.4204	69.6	20	0.7945

EATING TIME (Te)

MU	1.4273	1.4521	0.0902	259.2	68	0.7971
CO	-1.0369	2.1746	0.1835	140.5	72	0.6775
WH	-2.7499	3.0680	0.3786	65.8	22	0.7665
CA	-1.0533	2.5458	0.3881	43.0	20	0.7050

HANDLING TIME (Ht)

MU	0.9812	1.6791	0.0846	393.8	68	0.8565
CO	-3.1059	2.9408	0.2391	151.3	72	0.6837
WH	-3.1746	3.3430	0.3493	91.6	22	0.8203
CA	-1.8545	3.0268	0.3398	79.3	20	0.8150

Table 4.5. Summary of regression analyses for breaking, eating and handling time and prey species for medium (80-90 mm carapace width) *C.novaezelandiae*. All lines transformed using natural logarithm.

Prey : MU = mussel, CO = cockle,
WH = whelk, CA = catseye

a = Y-Intercept, b = Slope,
SE_b = Standard Error of the Slope,
F = Regression Significance, n = Sample Size,
r^2 = Correlation Coefficient.

BREAKING TIME (Tb)

Prey	a	b	SE^b	F	n	r^2
MU	-2.9675	2.4667	0.1759	196.7	58	0.7784
CO	-11.789	5.6858	0.4711	145.7	69	0.6849
WH	-8.2614	4.6394	0.3587	167.3	45	0.7956
CA	-1.5311	3.0132	0.6167	23.8	15	0.6574

EATING TIME (Te)

MU	-0.9450	2.7136	0.5360	25.6	15	0.6635
CO	-4.6270	3.3849	0.2933	133.3	69	0.6700
WH	-8.4438	4.8265	0.3536	186.5	45	0.8125
CA	-1.0533	2.5458	0.3881	43.0	20	0.7050

HANDLING TIME (Ht)

MU	1.4129	1.6127	0.0934	297.9	58	0.8418
CO	-7.9287	4.6963	0.3346	197.0	69	0.7462
WH	-6.9251	4.5431	0.3210	200.3	45	0.8233
CA	-0.6048	2.8989	0.5342	29.45	15	0.6938

Table 4.6. Summary of regression analyses for breaking, eating and handling time and prey species for small (55-65 mm carapace width) *C.novaezelandiae*. All lines transformed using natural logarithms.
Prey : MU = mussel, CO = cockle,
WH = whelk, CA = catseye

a = Y-Intercept, b = Slope,
SE_b = Standard Error of the Slope,
F = Regression Significance, n = Sample Size,
r^2 = Correlation Coefficient.

BREAKING TIME (Tb)

Prey	a	b	SE^b	F	n	r^2
MU	-2.2118	2.4617	0.6181	175.5	59	0.7550
CO	-7.5771	4.6619	0.4891	90.8	48	0.6639
WH	-8.4583	5.0504	0.6521	60.0	25	0.7228
CA	-4.2040	4.2105	0.5685	54.9	10	0.8727

EATING TIME (Te)

MU	0.2140	2.0127	0.3808	309.4	59	0.8444
CO	-3.1343	3.0833	0.2296	180.4	48	0.7968
WH	-10.413	5.7900	0.9269	39.0	24	0.6494
CA	2.8267	1.7446	0.4377	15.9	10	0.6750

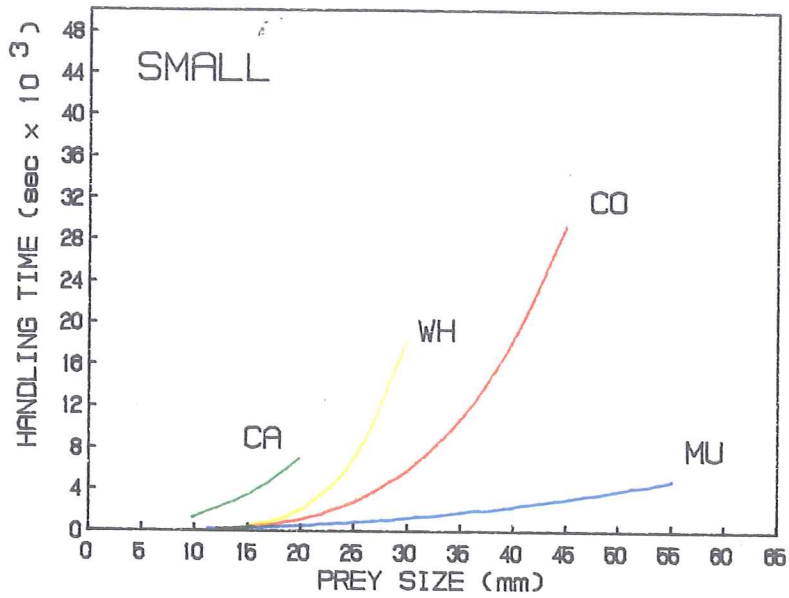
HANDLING TIME (Ht)

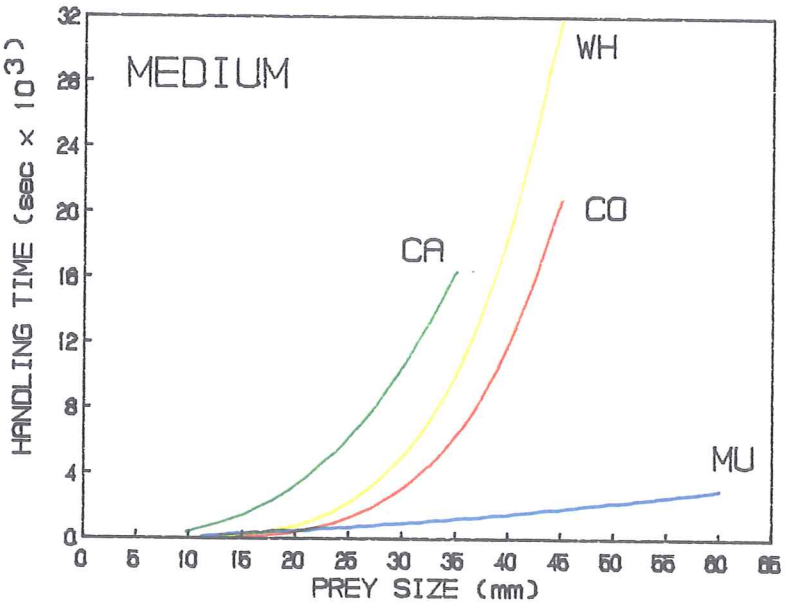
MU	0.1356	2.1538	0.1172	337.6	59	0.8556
CO	-4.8645	3.9810	0.3435	134.3	48	0.7449
WH	-8.5587	5.3987	0.1792	69.6	24	0.7598
CA	1.6493	2.3990	0.3612	44.1	10	0.8465

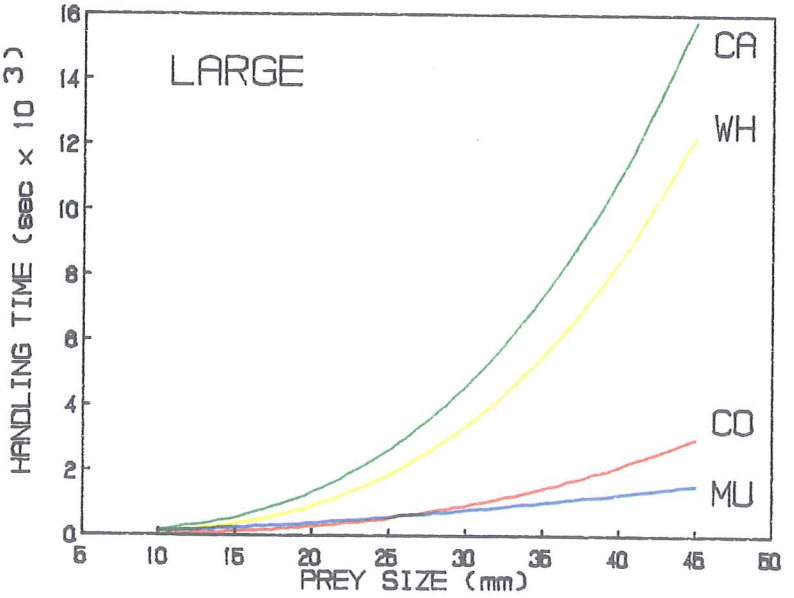
Figure 4.6. Handling time and prey size of each prey species for small (top), medium (centre) and large (bottom) crabs. Curves derived from single regressions of handling time given in Tables 4.4, 4.5 & 4.6.

KEY

CA = Catseye.
CO = Cockle.
MU = Mussel.
WH = Whelk.


SMALL
HANDLING TIME (sec x 10 3)
PREY SIZE (mm)
CA
WH
CO
MU


MEDIUM
HANDLING TIME (sec x 10 3)
PREY SIZE (mm)
CA
WH
CO
MU


LARGE
HANDLING TIME (sec x 10 3)
PREY SIZE (mm)
CA
WH
CO
MU

consume flesh increased rapidly with increasing prey size. This was a consequence of utilizing different attack techniques following the failure of a previous attempt. Eating time was expected to vary as the cube of shell length, reflecting the volume of flesh ingested (Elner and Hughes, 1978). However, eating times were variable dependent on crab size and prey species. Nevertheless, eating times generally increased with prey size. The rates of eating time for bivalves were generally lower than gastropods.

Analysis of covariance between handling time components and crab size for each prey species is shown in Tables 4.7, 4.8, 4.9 & 4.10. Components of handling time generally decreased with increased crab size. Thus opening and eating time for a given sized prey decreased from small to medium to large crabs. However, when dealing with small prey (10-15 mm shell length or height), handling time components were similar regardless of crab size.

For a given sized prey, handling times were significantly different between prey species for small, medium and large crabs (Table 4.11; Figure 4.6). These differences were greatest for medium to large prey (> 25 mm shell length or height). For small prey, however, handling times were very similar regardless of prey species given. Small, medium and large crabs exhibited shortest handling times for mussels, followed by cockles, then whelks, while catseyes had the greatest handling time of all prey species. For large crabs two distinct groups, each with similar handling rates, were evident with increased prey size;

Table 4.7. Anaylsis of Covariance statistics for breaking, eating and handling time and crab size when presented with *Mytilus edulis aoteanus*. Transformed data using $\log_{10}$.

BREAKING TIME

Source Of Variation	DF	SS	MS	F	P	
Equality of Adj. Means	2	5.8636	2.9317	26.4899	0.000	***
Equality of Slopes						
All Covariance, All Groups	2	0.2372	0.1186	1.0725	0.344	NS
Error	183	20.2373	0.1106			

EATING TIME

Source Of Variation	DF	SS	MS	F	P	
Equality of Adj. Means	2	2.7052	1.3526	30.7395	0.000	***
Equality of Slopes						
All Covariance, All Groups	2	1.0947	0.5473	14.2157	0.000	***
Error	183	7.0458	0.0385			

HANDLING TIME

Source Of Variation	DF	SS	MS	F	P	
Equality of Adj. Means	2	0.2545	0.1273	36.6155	0.000	***
Equality of Slopes						
All Covariance, All Groups	2	0.0339	0.0169	5.0858	0.007	***
Error	183	0.6091	0.0033			

Table 4.8. Anaylsis of Covariance statistics for breaking, eating and handling time and crab size when presented with *Chione stutchburyi*. Transformed data using $\log_{10}$.

BREAKING TIME

Source Of Variation	DF	SS	MS	F	P	
Equality of Adj. Means	2	34.0795	17.0398	111.1269	0.000	***
Equality of Slopes						
All Covariance, All Groups	2	1.4185	0.7092	4.8352	0.009	***
Error	167	24.4953	0.1467			

EATING TIME

Source Of Variation	DF	SS	MS	F	P	
Equality of Adj. Means	2	3.7655	1.8828	39.4624	0.000	***
Equality of Slopes						
All Covariance, All Groups	2	1.1753	0.5876	14.2475	0.000	***
Error	167	6.8876	0.0412			

HANDLING TIME

Source Of Variation	DF	SS	MS	F	P	
Equality of Adj. Means	2	13.0342	6.5171	83.0005	0.000	***
Equality of Slopes						
All Covariance, All Groups	2	2.1266	1.0633	15.9359	0.000	***
Error	167	11.1430	0.0667			

Table 4.9. Anaylsis of Covariance statistics for breaking, eating and handling time and crab size when presented with *Cominella maculosa*. Transformed data using $\log_{10}$.

BREAKING TIME

Source Of Variation	DF	SS	MS	F	P	
Equality of Adj. Means	2	2.7425	1.3713	14.4420	0.000	***
Equality of Slopes						
All Covariance, All Groups	2	0.1779	0.0890	0.9357	0.396	NS
Error	88	8.3676	0.0951			

EATING TIME

Source Of Variation	DF	SS	MS	F	P	
Equality of Adj. Means	2	0.3917	0.1958	1.4770	0.234	NS
Equality of Slopes						
All Covariance, All Groups	2	1.5493	0.7747	6.5650	0.002	***
Error	88	7.0458	0.0385			

HANDLING TIME

Source Of Variation	DF	SS	MS	F	P	
Equality of Adj. Means	2	1.0366	0.5183	5.9565	0.004	***
Equality of Slopes						
All Covariance, All Groups	2	0.9472	6.0543	6.0543	0.003	***
Error	88	6.8838	0.0782			

Table 4.10. Anaylsis of Covariance statistics for breaking, eating and handling time and crab size when presented with *Turbo smaragdus*. Transformed data using $\log_{10}$.

BREAKING TIME

Source Of Variation	DF	SS	MS	F	P	
Equality of Adj. Means	2	3.0815	1.5407	26.2985	0.000	***
Equality of Slopes						
All Covariance, All Groups	2	0.1244	0.0622	1.0648	0.355	NS
Error	39	2.2777	0.0584			

EATING TIME

Source Of Variation	DF	SS	MS	F	P	
Equality of Adj. Means	2	2.2981	1.1491	25.8564	0.000	***
Equality of Slopes						
All Covariance, All Groups	2	0.0877	0.0438	0.9856	0.382	NS
Error	39	1.7344	0.0445			

HANDLING TIME

Source Of Variation	DF	SS	MS	F	P	
Equality of Adj. Means	2	2.5574	1.2787	34.0832	0.000	***
Equality of Slopes						
All Covariance, All Groups	2	0.0369	0.0185	0.4797	0.623	NS
Error	39	1.5013	0.0385			

Table 4.11. Analysis of Covariance statistics for handling time and all four prey species for large (105-115 mm carapace width), medium (80-90 mm) and small (55-65 mm) *C.novaezelandiae*. Transformed data using $\log_{10}$.

LARGE

Source Of Variation	DF	SS	MS	F	P	
Equality of Adj. Means	3	12.968	4.3227	74.2627	0.000	***
Equality of Slopes						
All Covariance, All Groups	3	1.841	0.6137	12.8961	0.000	***
Error	158	7.530	0.0477			

MEDIUM

Source Of Variation	DF	SS	MS	F	P	
Equality of Adj. Means	3	12.9263	4.3088	39.957	0.000	***
Equality of Slopes						
All Covariance, All Groups	3	8.9778	2.9926	50.3065	0.000	***
Error	179	10.6482	0.0595			

SMALL

Source Of Variation	DF	SS	MS	F	P	
Equality of Adj. Means	3	9.8813	3.2938	38.3741	0.000	***
Equality of Slopes						
All Covariance, All Groups	3	3.4718	1.1573	18.7664	0.000	***
Error	133	8.2016	0.0017			

mussels/cockles and whelks/catseyes. However, for medium and small crabs, as prey size increased, handling time of mussels increased linearly, while time taken to handle cockles quickly accelerated to a rate similar to gastropods.

Profitability

The yield of flesh was related to the size of cockle, whelk and catseye by the dry weight-wet weight regression equations shown in Table 4.12. Also shown is the energetic content of flesh for each prey species.

The rates of prey energetic value over handling time (E/Th) for mussels and whelks measures profitability and shows a monotonic increasing or decreasing curves with prey size respectively (Figures 4.7 & 4.8). For mussels, as prey size increased, profitability increased linearly for large, medium and small crabs. Comparison of all three lines showed they were significantly different ($F=21399$, $df=2,23$, $P<0.001$ for slopes, $F=84.2$, $df=2,23$, $P<0.001$ for adjusted means). This was particularly apparent for medium and large mussels.

Whelks, however, showed a decreasing profitability curve with increased prey size for medium and small crabs. Yet profitability remained approximately constant for large crabs. Similarly with mussels, profitability curves for different crab size groups were significantly different ($F= 2543.4$, $df=2,21$, $P<0.001$ for slopes, $F=18.26$, $df=2,23$, $P<0.001$ for adjusted means).

Table 4.12. Summary of regression equations of dry weight-wet weight for cockle, whelk, catseye and mussel. All lines transformed using natural logarithms.
Table includes flesh calorific value for each prey species.

a = Y-Intercept, b = Slope, SE_b = Standard Error of the Slope, F = Regression Significance, n = Sample Size,
r^2 = Regression Co-efficient,
x Kj g^{-1} = Mean Calorific Value,
SD = Standard deviation.

Regression equation and calorific value given by Davidson (1984).

PREY SPECIES	a	b	SE_B	F	n	r^2	x Kj g^{-1}	SD	n
Chione stutchburyi	-10.45	2.67	0.18	208.2	30	0.88	14.423	1.34	10
Cominella maculosa	-12.08	3.27	0.12	768.2	30	0.97	16.988	0.13	10
Turbo smaragdus	-12.26	3.48	0.13	708.6	30	0.96	13.580	1.23	10
Mytilus edulis aoteanus##	-10.99	2.78	-	-	59	0.95	19.500	0.40	10

Figure 4.7. Profitability curves of Mytilus edulis aoteanus for small, medium and large crabs.
Curves derived from the equation :
Prey energy value/Handling time.

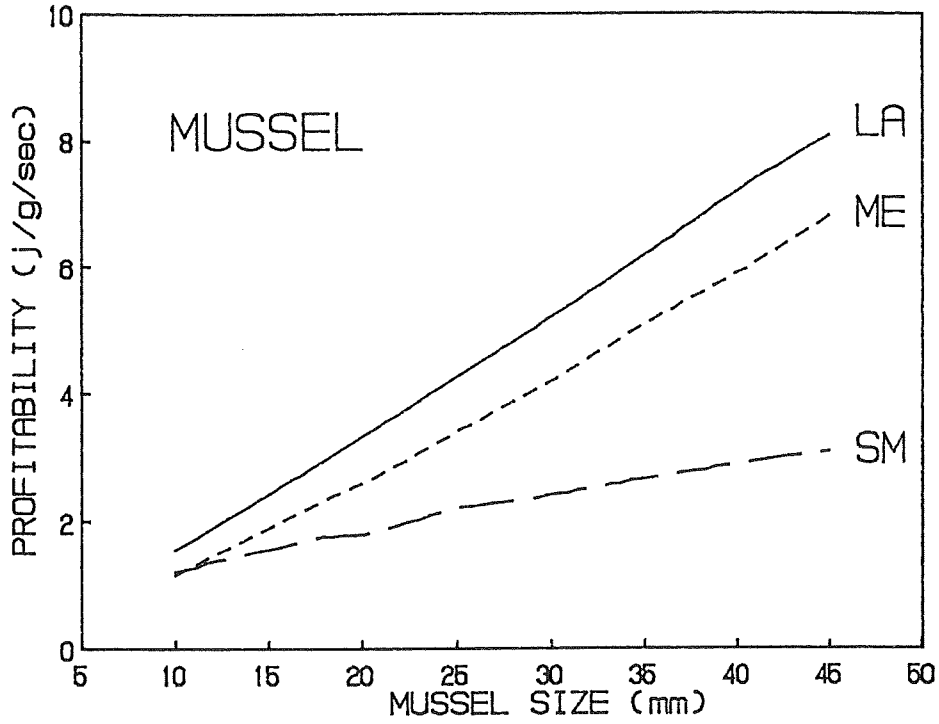
KEY

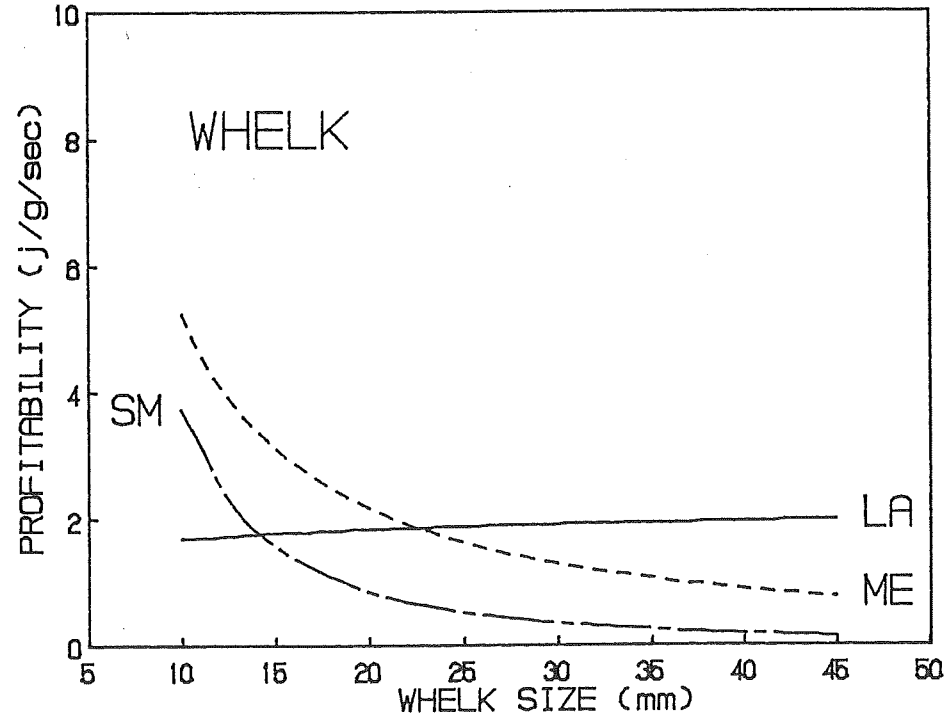
SM = Small Crabs.
ME = Medium Crabs.
LA = Large Crabs.

Figure 4.8. Profitability curves of Cominella maculosa for small, medium and large crabs.
Curves derived from the equation :
Prey energy value/Handling time.

KEY

SM = Small Crabs.
ME = Medium Crabs.
LA = Large Crabs.


MUSSEL
LA
ME
SM
PROFITABILITY (j/g/sec)
MUSSEL SIZE (mm)
0
2
4
6
8
10
5
10
15
20
25
30
35
40
45
50


WHELK
SM
LA
ME
PROFITABILITY (j/g/sec)
WHELK SIZE (mm)
0
2
4
6
8
10
5
10
15
20
25
30
35
40
45
50

Profitability curves comparing prey species for small, medium and large crabs are shown in Figure 4.9. Profitabilities of four prey species, mussels, whelks, cockles and catseyes were significantly different for large crabs ($F=2919.0$, $df=3,24$, $P=0.000$ for slopes, $F=16.68$, $df=3,24$, $P=0.000$ for adjusted means). Profitability curves of mussels increased linearly with prey size for all three crab sizes, while cockles showed a decreasing curve. Gastropods exhibited lower profitability curves with decreasing or constant profitability with prey size.

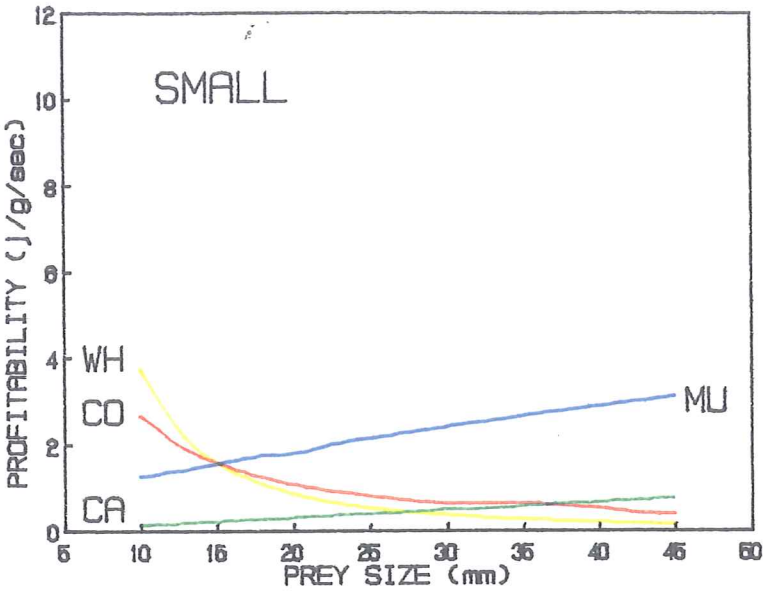
Prey-Size Selection Experiments

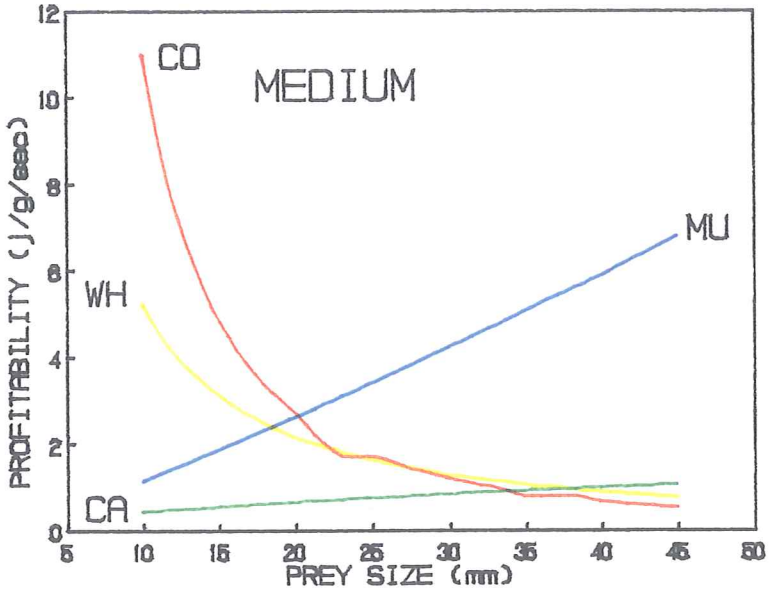
When presented with five categories of mussels as potential prey in high abundance, there was individual variability between crabs of the same size and individual crabs from day to day. However, the mean data suggests that crabs significantly foraged on mussels of a particular size ($X^2=124.65$, 65.29 and 107.29, $df=4$, $P<0.001$ for small, medium and large crabs respectively, Figure 4.10). Moreover the preferred mussel size chosen decreased with decreased crab size ($X^2=50.29$, $df=8$, $P<0.001$). Large crabs consumed mussels of all size classes, however they showed a preference for mussels between 20-30, 35-45 and 50-60 mm. Medium crabs preferred medium size mussels (20-30 and 35-45 mm), however, 5-15 and 50-60 mm length mussels were also taken. However, no 65-75 mm mussels were consumed. Small crabs preferred small mussels size classes (5-15 and 20-30 mm), but did not eat large mussels.

Figure 4.9. Profitability curves for each prey species for small (top), medium (centre) and large (bottom) crabs. Curves derived from the equation : Prey energy value/Handling time.

KEY

CA = Catseye.
CO = Cockle.
MU = Mussel.
WH = Whelk.


SMALL
PROFITABILITY (J/g/sec)
PREY SIZE (mm)
WH
CO
CA
MU


MEDIUM
PROFITABILITY (J/g/sec)
PREY SIZE (mm)
CO
MU
WH
CA

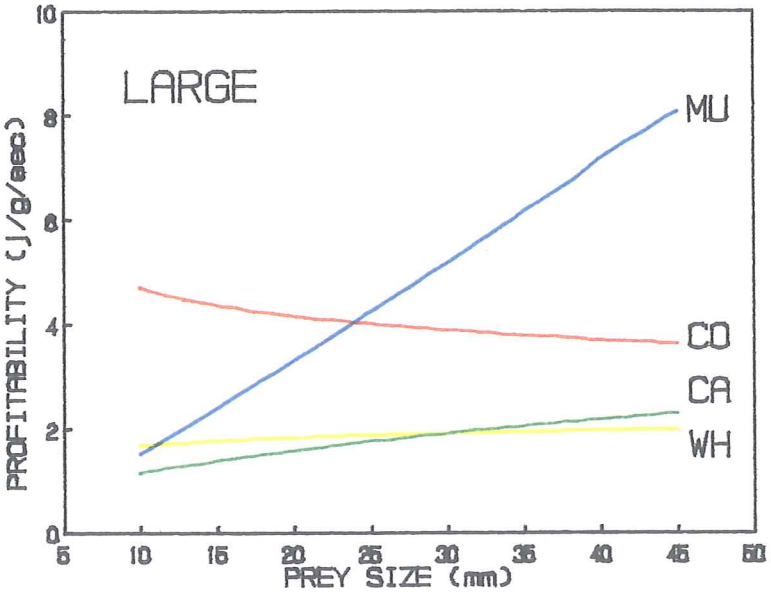
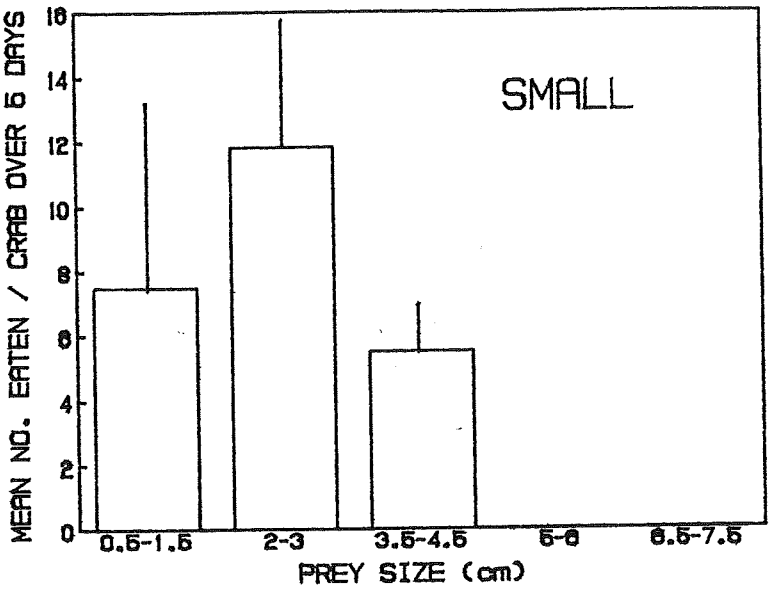
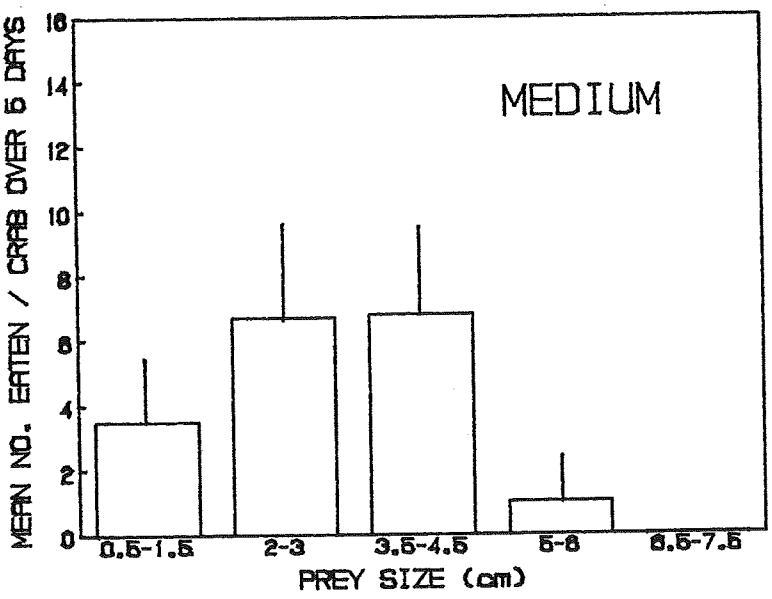
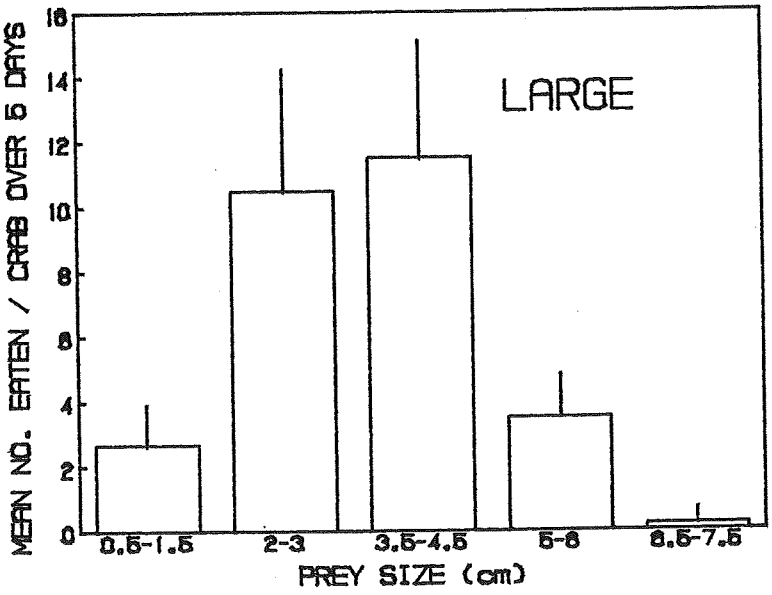

LARGE
PROFITABILITY (J/g/sec)
PREY SIZE (mm)
MU
CO
CA
WH

Figure 4.10. Size-selection of Mytilius edulis aoteanus.
Mean number of mussels eaten per crab over 5 days for small (n=6, top), medium (n=6, centre) and large (n=6, bottom) crabs.
Standard deviations are shown.


SMALL
MEAN NO. EATEN / CRAB OVER 5 DAYS
0
2
4
6
8
10
12
14
16
0.5-1.5
2-3
3.5-4.5
5-6
6.5-7.5
PREY SIZE (cm)


MEDIUM
MEAN NO. EATEN / CRAB OVER 5 DAYS
0
2
4
6
8
10
12
14
16
0.5-1.5
2-3
3.5-4.5
5-6
6.5-7.5
PREY SIZE (cm)


LARGE
MEAN NO. EATEN / CRAB OVER 5 DAYS
0
2
4
6
8
10
12
14
16
0.5-1.5
2-3
3.5-4.5
5-6
6.5-7.5
PREY SIZE (cm)

Crabs also showed distinct preferences for particular whelk size classes (X^2=31.7, 31.3,and 14.4, df=3, P<0.001 for small, medium and large crabs, respectively, Figure 4.11). These size preferences also decreased with decreasing crab size (X^2=59.54, df=6, P<0.001). Large crabs consumed all size classes but preferred mainly large whelks (25-45 mm shell height). However, medium and small crabs did not consume whelks over 35 mm; instead, they fed on mainly small whelks between 5-25 mm.

Consumption Rates

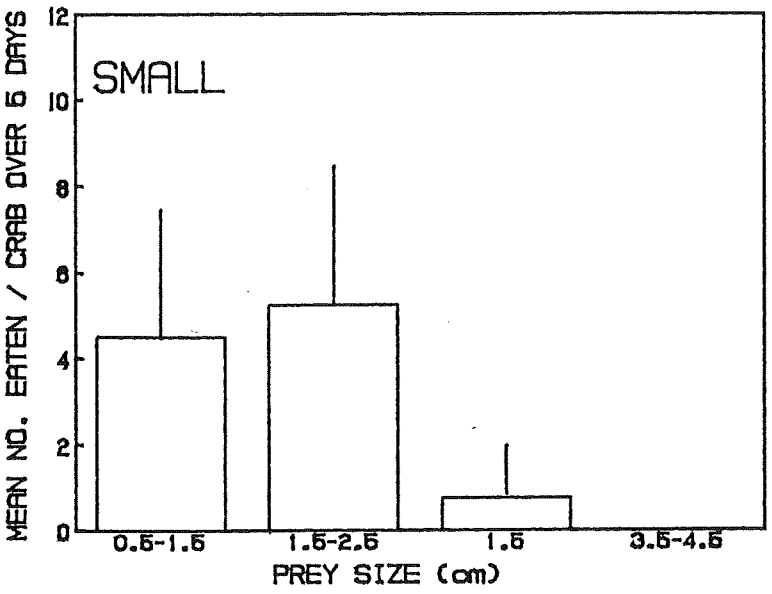
The mean number of mussels and whelks consumed and energy intake per crab over five days is shown in Table 4.13. Consumption rates of small, medium and large crabs when presented with mussels or whelks were not found to be significantly different (F=2.41, df=2,15, P=0.1241, F=1.13, df=2,9, P=0.364 for mussels and whelks respectively). Feeding rates, in terms of energy intake (j/crab/5 days) increased substantially with crab size, and was found to be significantly different between crab size classes (F=13.22, df=2,15, P<0.001, F=26.43, df=2,9, P<0.001 for mussels and whelks respectively).

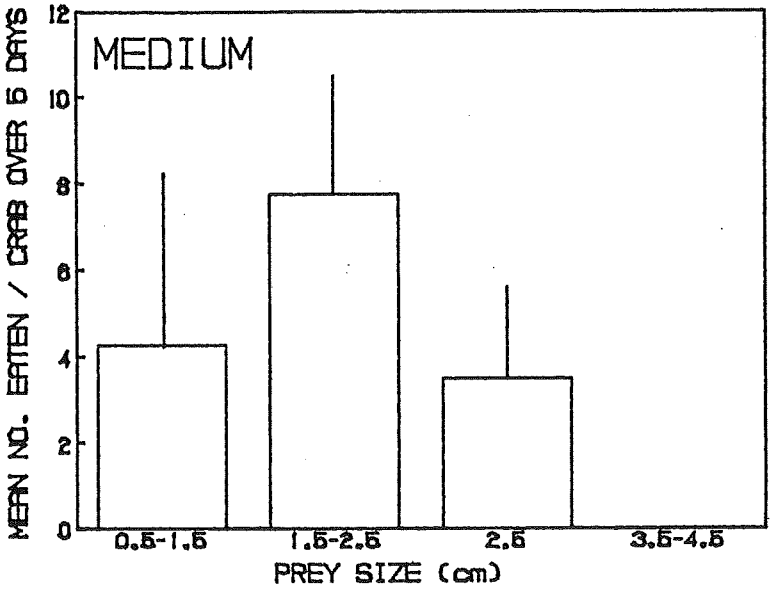
Crabs consumed considerably fewer whelks than mussels. Energy intake for small, medium and large crabs was considerably higher when feeding on mussels in comparison to whelks.

Prey-Species Selection Experiments

Large crabs presented with equal numbers of mussels and cockles of three different size classes showed distinct prey

Figure 4.11. Size-selecion of Cominella maculosa. Mean number of whelks eaten per crab over 5 days for small (n=4, top), medium (n=4, centre) and large (n=4, bottom) crabs.
Standard deviations are shown.


SMALL
MEAN NO. EATEN / CRAB OVER 5 DAYS
0
2
4
6
8
10
12
0.5-1.5
1.5-2.5
1.5
3.5-4.5
PREY SIZE (cm)


MEDIUM
MEAN NO. EATEN / CRAB OVER 5 DAYS
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2
4
6
8
10
12
0.5-1.5
1.5-2.5
2.5
3.5-4.5
PREY SIZE (cm)

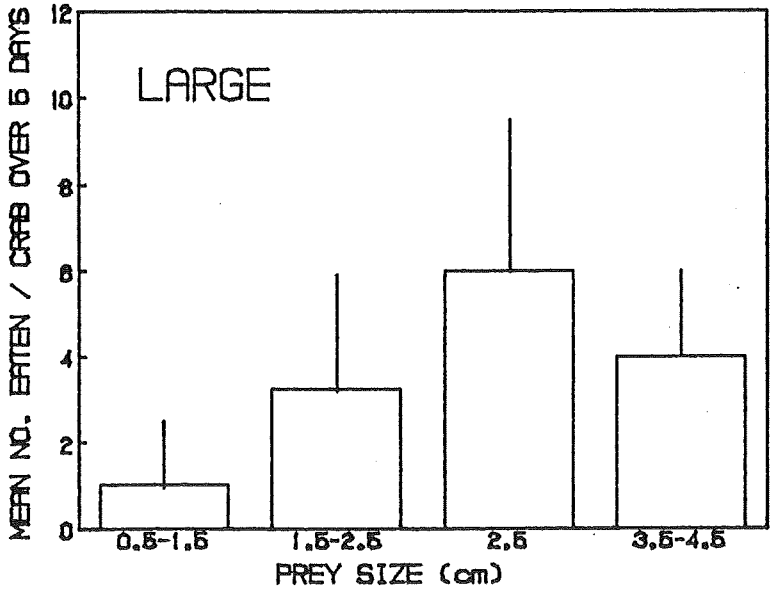

LARGE
MEAN NO. EATEN / CRAB OVER 5 DAYS
0
2
4
6
8
10
12
0.5-1.5
1.5-2.5
2.5
3.5-4.5
PREY SIZE (cm)

Table 4.13. Mean consumption rates and energy intake of mussels and whelks per crab over 5 days for small (55-65 mm carapace width), medium (80-90 mm) and large (105-115 mm) *C.novaezelandiae*.

	CRAB SIZE		
	SMALL	MEDIUM	LARGE
	Mytilus edulis aoteanus		
$\bar{x}$ mussels eaten crab^{-1} 5 days	24.8 ± 10.5	18.0 ± 7.3	28.3 ± 7.3
$\bar{x}$ joules crab^{-1} 5 days	118.7 ± 53.4	182.3 ± 97.0	367.4 ± 89.1
	Cominella maculosa		
$\bar{x}$ whelks eaten crab^{-1} 5 days	10.5 ± 5.0	15.5 ± 5.3	14.5 ± 6.5
$\bar{x}$ joules crab^{-1} 5 days	9.8 ± 3.2	19.9 ± 7.7	58.3 ± 21.4

species preferences (Table 4.14). When given a choice of small prey (10-15 mm) cockles were preferred (X^2=17.03, df = 3, P<0.001). No species preference was evident between medium size (28-33 mm) prey (X^2=0.9141, df = 3, P=0.914). However, for large prey (40-45 mm), mussels were preferred over cockles (X^2=128.0, df = 3, P<0.001).

Table 4.14. Mean number of prey eaten per crab over 5 days when presented with a choice of small (10-15 mm), medium (28-35 mm) and large (40-45 mm) mussels and cockles to large *C.novaezelandiae*.

Prey : MU = Mussel.
CO = Cockle.

SD = Standard Deviation, n = Number of crabs used,
X^2 = Chi Square, DF = Degrees of Freedom,
P = Probability.

PREY SIZE	PREY SPECIES	$\bar{X}$ EATEN	SD	n	X^2	DF	P	
Small	MU	24.8	15.3	4	17.03	1	0.001	***
	CO	48.3	2.1	4				
Medium	MU	30.8	2.7	4	0.05	1	0.914	NS
	CO	29.0	3.3	4				
Large	MU	32.0	7.8	4	128.0	1	0.001	***
	CO	0.0	0.0	4				

DISCUSSION

The predatory behaviour of Cancer novaezelandiae feeding on mussels, cockles, whelks and catseyes was influenced by many factors including crab size, prey size, species and profitability. In the following discussion, components of feeding will be discussed separately, but the processes that determine feeding should not be viewed as separate entities, but rather as a complex, inter-related system.

Laboratory experiments demonstrated that C.novaezelandiae readily accepted and consumed a variety of mollusc species. Once prey was presented, crabs employed distinct opening techniques, and handling times, consumption rates and critical upper and lower prey limit were all dependent on crab size, prey size and species. When presented with a choice of prey size or species, C.novaezelandiae clearly exhibited distinct preferences.

Initially, the detection of prey was most likely chemosensory rather than visual, as immediately after prey was presented an increased rate in antennular flickering rate was immediately apparent for all prey species. This increase in rate was no doubt a response to the presence of body fluids released from the prey. Soon after, the crab quickly orientated towards the vicinity of the prey. Prey recognition behaviour exhibited by C.novaezelandiae is typical for most brachyurans. Similar behaviours has been observed for Ovalipes guadulpensis (Caine, 1974); Ovalipes catharus (Davidson, 1986); Callinectes sapidus

(Blundon and Kennedy, 1982); Ozius truncatus (Chilton and Bull, 1986) and Cancer pagurus (Lawton and Hughes, 1985). Cancer magister when presented with bivalve Protothaca staminea extract of 10^{-10} g/l showed an abrupt change in antennular orientation and increased flickering rate (Pearson, et.al., 1979). The authors, however, did not state whether such behaviour aided recognition of prey presence or particular prey species.

Although chemosensory behaviour was the first response to prey, it most likely served only to recognise prey presence. Species determination and size recognition were most likely performed by actual physical contact with the shell. Once prey has been caught, it was usually manipulated extensively using chelipeds and walking legs by rotating the shell continuously in all planes. This manipulation acted to ensure that all parts of the shell came into contact with the appendages, and mouthparts. Physical contact of the shell therefore, was most likely the principle method employed by crabs to recognise prey species and feasibility of successfully opening the shell.

Opening Techniques

The method employed by C.novaezelandiae to open the shell and extract flesh depended upon prey size, species and crab size. Once attempts to break prey began, different techniques were progressively employed depending on the success of previous attempts. When opening mussels and cockles, direct crushing was immediately attempted regardless of prey size. However, this technique was only successful on small shells. Subsequently,

different methods were used in progressive fashion until one method proved successful. Splitting or wedging of the umbone proved the most successful technique to open large bivalves. When handling gastropods, however, different techniques were employed. Direct crushing was the first method employed but was only successful on small whelks. Different techniques were also tried and breakage of the aperture lip proved the most successful.

Similar techniques for opening bivalves and gastropods described here for C.novaezelandiae have been observed for a number of brachyurans, particularly portunids feeding on similar prey species. O.catharus when presented with individual Mytilus edulis aoteanus was shown to exhibit five opening techniques and generally utilized a characteristic attack sequence (Davidson, 1986). Moreover the techniques employed were dependent on prey size with small mussels being crushed directly, whilst larger sizes were opened by splitting of the umbone, and chipping of the posterior edge. Similar results were also observed by Wear (1984) for O.catharus. Carcinus maenas has been reported to use five distinct methods to attack mussels and three methods to attack dogwhelks Nucella lapillus (Cunningham and Hugh, 1984; see also Feare, 1970; Elner, 1978; Ameyaw-akumfi and Hughes, 1987). The five methods used by O.catharus and C.maenas correspond to those observed for C.novaezelandiae when presented with identical sized prey species. Juvenile C.magister when presented with the bivalve Transennella tantilla were also observed to show distinct opening techniques dependent both on prey size and success of previous attempts. Similar observations have been made for Liocarcinus

puber (Hughes and Seed, 1981) and Ovalipes punctatus (Du Preez, 1984) when fed on a variety of bivalves.

For C.novaezelandiae the success of a particular opening technique for both bivalves and gastropods appeared to be largely dependent on prey size. However, crab size was also an important factor as larger crabs are capable of exerting stronger forces and able to directly crush larger prey than small crabs. Therefore the employment of more time consuming techniques by large crabs were only required to open larger, more robust prey. This was the case for both cockles and whelks. However, when presented with mussels and catseyes, crab size was not an important factor in determining success of a particular opening technique. Instead as cockle and whelk size (and invariably strength) increased, different methods required to break prey were employed equally by crabs regardless of crushing capabilities.

Unfortunately, however, the influence of crab size as a factor determining mollusc opening success has been neglected in previous studies. Blundon and Kennedy (1982) demonstrated that small (< 80 mm carapace width) C.sapidus could not open large (90 mm) Mya arenaria by direct crushing, as do larger crabs. Instead small crabs resorted to chipping of the shell edge in order to prise shell valves apart. Whereas a 45 mm blue crab was only able to crush a 45 mm clam, but had to resort to edge chipping a 52 mm clam. Large C.sapidus (> 120 mm carapace width), however, were able to direct crush even the largest M.arenaria (> 90 mm).

The similarity in opening techniques observed between portunids and C.novaezelandiae in the present study is an interesting feature with respect to chelae morphology. The chelipeds of portunids are heterochelic, the left and right are different in size and shape. More importantly, each chela performs particular functions, be it crushing, cutting or holding (see Chapter Three). However, C.novaezelandiae is homeochelous, both chela are identical in size and shape and both perform identical functions. Therefore it is interesting that similar methods are used by portunids and C.novaezelandiae to open bivalves and gastropods. It appears therefore that opening techniques described here are general features amongst large, predatory crabs. Moreover, C.novaezelandiae did not prefer one particular cheliped to detect, hold, attack or consume prey. Whereas the cutter and crusher chela of portunid crabs are associated with specific roles. Therefore, it is not cheliped morphology that determines opening techniques required to successfully open a particular species of mollusc, but rather stereotyped crab behaviour and prey size.

Handling Times

As prey size increased, handling time by C.novaezelandiae increased rapidly for all three crab sizes investigated. Breaking time accelerated with shell length or height probably due to complex interactions of shell shape and strength (Elner and Hughes, 1978). As bivalves and gastropod shells increase in size, shell thickness and geometric robustness increased. Thus greater

physical stress was required by C.novaezelandiae to break the shell. Hence as shell size increased, handling times became considerably greater due to the employment of techniques involving either chipping or splitting small regions of shell, rather than directly crushing the entire shell.

Flesh volume increases with prey size as a cube function (Elner and Hughes, 1978). Therefore it might be expected that eating times would increase as a cube. However, C.novaezelandiae exhibited variable eating times, suggesting eating time was not only a function of shell length, but other factors including chela strength and manipulatory ability.

Similar findings have been demonstrated for a number of crab species, particularly portunids when presented with bivalves (Elner and Hughes, 1978; Elner and Raffaelli, 1980; Jubb, Hughes and ap Rheinallt, 1983; ap Rheinallt, 1986; Davidson, 1986) and gastropods (Chilton and Bull, 1986). C.maenas has featured in a number of these studies and it has been shown that when presented with various sized M.edulis, breaking times increased asymptotically with shell length, with large crabs taking less time than smaller crabs to handle prey (Elner and Hughes, 1978). These handling times were attributable to a complex interaction of shell strength, chela strength and changing mechanical advantage. Eating times were variable but showed an exponential increase and again other factors were involved. Ap Rheinallt and Hughes (1985) found similar findings for L. puber. They found a positive correlation for shortest breaking time and chela height

and concluded that opening of large mussels was related directly to mechanical constraints of the chela. Differences in handling time observed between male and female L.puber illustrated further the importance of chela size on handling. For a given crab size, male crabs showed shorter handling times than female crabs, which could be directly related back to their larger chela size.

Cancer pagurus when presented with two species of gastropod N.lapillus and Littorina littorea also showed increased handling times with increased prey size, and for a given prey size times were longer for smaller crabs (Lawton and Hughes, 1985). However, unlike portunid crabs, sex was found not to be a significant determinant of breaking time. Instead crab size and prey size were considered the principle determinants constraining handling time. Although the influence of crab sex on handling time was not an aspect of this study, it would be expected not have an significant affect on prey handling time as male and female C.novaezelandiae possess similar chela with respect to size and shape.

Comparisons of breaking times between different crab species for medium and small M.edulis are shown in Table 4.15. Opening times shown by C.novaezelandiae correspond closely to those cited for portunid crabs when presented with small mussels. However, comparisons for larger mussels show significant differences in breaking time and crab species. Thus as mussel size increased, the time required for portunid crabs to open mussel shell increased at a much faster rate than for C.novaezelandiae.

Table 4.15 Comparisons of breaking time (sec) of Mytilus edulis between small and medium portunid and cancer crabs.

CRAB SPECIES	CRAB SIZE (mm)	BREAKING TIME (sec) SMALL (25 mm)	LARGE (35 mm)
Carcinus maenas #[1]	50-55	800	---
	70-75	300	400
Ovalipes catharus #[2]	50-55	1200	----
	70-75	120	600
Liocarcinus puber #[3]	70-80	613-1681	937-1413
Cancer novaezelandiae	55-65	300	690
	80-90	144	330

#[1] Elner and Hughes (1978)
#[2] Davidson (1986)
#[3] ap Rheinallt (1986)

Differences in breaking times between cancrid and portunid crabs are clearly related to chela morphology and strength. Cancrid crabs which possess large, monomorphic chela are able to exert stronger compressive forces during crushing and thus open prey more quickly (Warner and Jones, 1976). Hence, while C.novaezelandiae may not be able to hold and manipulate prey efficiently in comparison with portunids, it is able to break mussel shells at a faster rate.

Handling times of all four prey species used in this study decreased considerably as crab size increased. This was a direct function of chela strength, as larger crabs are capable of exerting greater chelal forces (Warner and Jones, 1976). However, size-related differences in handling times only became significant for medium to large prey sizes. For small prey, handling times were similar for all crabs. Thus with respect to crab size, there is a "trade off" between chela strength and chela dexterity. The upper size limit of successfully opened prey is determined by the interaction of shell robustness and chela strength and gape. Hence large, stronger crabs have a distinct advantage over their smaller, weaker counterparts and thus are capable of feeding on larger prey sizes. It was not surprising, therefore, that maximum size of all four prey species increased with crab size. However, the lower size limit is not a function of strength, but rather chela dexterity and manipulative ability. The chelipeds of large C.novaezelandiae, although strong, are large and bulky and consequently are considerably clumsier and lack the ability to manipulate the shell efficiently. Small

crabs, while deficient in strength, possess greater chelal dexterity. Therefore whilst feeding on small prey sizes, small crabs although not possessing the ability to directly crush the shell are considerably more efficient in holding, rotating and applying force more precisely. It was not surprising that small crabs open small prey at a similar rate to that of medium and large crabs. Moreover, minimum prey size decreased with decreased crab size (cockles were the exception).

Similar findings have also been observed for Cancer pagurus (Lawton and Hughes, 1985); Carcinus maenas (Elner and Raffaelli, 1980); Liocarcinus puber (ap Rheinallt and Hughes, 1985); and Ozius truncatus (Chilton and Bull, 1986). These studies found that as crab size increased, the size range of prey successfully opened also increased. However the authors failed to mention whether minimum critical size was smaller for smaller crabs. Ap Rheinallt and Hughes (1985) found that prey size and time required for L.puber (31.0-86.0 mm carapace width) to pick up mussels were negatively correlated. This suggested that larger prey were easier to pick up because of the limited dexterity of the chela in dealing with small prey size. However the authors did not mention whether smaller crabs were more efficient in handling small prey than large crabs. The influence of mechanical factors determining critical prey size has been the principle explanation cited by the authors mentioned above.

Handling time was also influenced by the geometric shape of the prey, regardless of prey size. Generally the time taken to

handle bivalves (mussels and cockles) was considerably less than for gastropods (whelks and catseyes). The differences in time taken to handle bivalves and gastropods is no doubt a reflection of shell shape, infra-structure and thickness. Together these factors determine prey vulnerability.

Handling times were lowest for bivalves, particularly mussels. Bivalves are characteristically elongate in shape, and therefore crabs may be more efficient in handling them rather than a spherical or conical shape. Moreover, the shells of bivalves are generally thinner than gastropods and tend to have intrinsic "weak spots", particularly in regions prone to erosion eg. umbone tip (Elner, 1978). It is not surprising, therefore, that one particular method proves to be successful, as a result of concentrated efforts at the shell's weak spots. Gastropods on the otherhand are generally more conical in shape and considerably more robust. This shape prevents crushing of the spire as there is a tendency for the chela to slip over the spiral whorls. Therefore removal of the shell spire was only successful on large gastropods, yet handling times were considerably greater.

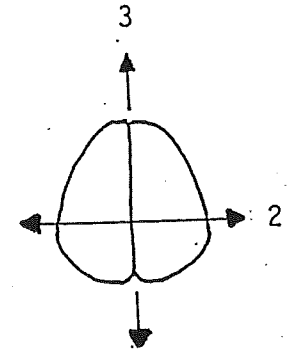
Few studies have demonstrated the strong influence of prey shell morphology on handling times. Elner and Hughes (1980) showed C.maenas exhibited faster breaking times when offered Littorina rudis (90-170 mm shell height) than when presented with Littorina nigrolineata (eg. 90, 450, 162 and 520 seconds for small and large L.rudis and L.nigrolineata, respectively). The

authors concluded that such a difference in opening times was a result of interspecific differences in shell thickness and aperture size. The time taken by O.truncatus to handle gastropod Nerita atramertosa was considerably longer than Bembicium nanum of a given height (Chilton and Bull, 1986). However, the authors failed to suggest any reasons for these differences.

Gastropods were more resistant to predation by C.novaezelandiae than bivalves for a number of reasons. The conical shape of gastropods limits the number of regions available for shell attack and penetration. For example, bivalves exhibit three available planes for crushing (Figure 4.12). While only two planes are available for crushing gastropods. Therefore more options are available to crabs attempting to open bivalves. It is not surprising, therefore, that five distinct opening techniques were exhibited by C.novaezelandiae when presented with bivalves, in comparison with only three recognisable techniques for gastropods.

Another feature of gastropods providing resistance to crab predation is shell robustness. Unlike bivalves, the internal geometry of gastropods involves coiling of shell wall. These act as cross-sectional walls which provide strong resistance in all planes of attack by crushing. Thus for C.novaezelandiae and other brachyurans direct crushing as an opening technique was only successful on small gastropods.

Figure 4.12. Planes available for crushing in bivalve Mytilus edulis aoteanus (left) and gastropod Cominella maculosa (right).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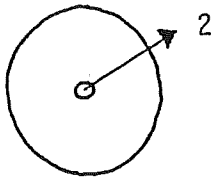
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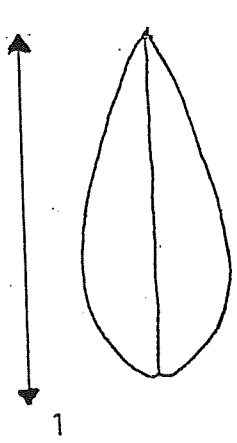
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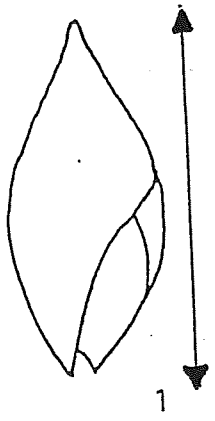

1

A characteristic of gastropods is the presence of an operculum which apart from acting as an anti-desiccation structure, also reduces the success of attacks by crabs. The operculum in species such as Turbo smaragdus is a thick calcified plate. Thus crabs attempting to expose snail flesh but incapable of directly crushing shell must first remove the operculum. However, once the operculum has contracted into the aperture, removal of the operculum is difficult. Therefore, the shape of the gastropod, its robust nature and operculum together act to form a very resistant shell structure to crab predation. However, C.novaezelandiae overcame these features somewhat by slowly "peeling away" piece by piece the apertural lip, thereby avoiding the need to crush or remove the operculum. This process of shell peeling is a time consuming process as flesh is not exposed immediately as it is with direct crushing. Instead, flesh is obtained after many slow concentrated attempts. Handling times were therefore considerably longer for Cominella maculosa and T.smaragdus than for the two bivalve species.

Profitability

Prey profitability or prey value estimates the theoretical amount of energy obtained by the crab per unit handling time. Profitability curves can be used to describe prey value for a particular prey size range or compare between different prey species. Using such calculations, predictions can be made with respect to the most profitable or "optimum" size or species that should be consumed by crabs when given a choice. Calculations of profitability curves derived from single regressions of energetic

yield and handling time of prey have been used in many studies (Elner and Hughes, 1978; ap Rheinallt, 1986; Davidson, 1986). However, Lawton and Hughes (1985) suggest these calculations fail to measure profitability accurately. Instead they favour calculations using individual handling times. However, it would be expected that such a method would result in highly variable, erroneous profitability values, particularly for larger prey sizes. This is the consequence of handling times which become variable due to increased influence of a number of factors (ie. employment of different opening techniques, change in prey shape) associated with increasing prey size. Furthermore Davidson (1986) stated that the use of individual handling times did not predict a profit peak at or near the critical size as expected. Therefore the use of single regression equations to estimate profitability is the most appropriate method to estimate the relationship between prey value and prey size.

Profitability curves for C.novaezelandiae feeding on M.edulis aoteanus increased monotonically with prey size. Thus the energetic content increased faster than the rate of handling time with mussel size. Therefore larger mussels are theoretically more profitable than smaller mussels as energy obtained is considerably greater than when feeding on smaller mussels. Furthermore, for a given mussel size, large crabs feed more profitably than smaller crabs, as the time required by the former to open and consume mussel is shorter than that taken by small crabs.

Profitability curves of mussels predicted for C.novaezelandiae differ markedly from those demonstrated for portunid crabs. Profitability curves for C.maenas showed distinct bell-shaped profitability curves peaking between 25 and 40 mm shell length (Elner and Hughes, 1978). Also it was predicted that the most profitable mussel size increased with crab size. For large crabs, the most profitable predicted mussel size was 30-35 mm shell length, whereas for medium and small crabs 25-30 and 15-25 mm mussels were most profitable. The shape of the curves could be explained by the low efficiency of crabs in handling very small and very large mussels, and therefore medium sized mussels gave highest energy intake. The profitability curves exhibited by O.catharus did not contain profit peaks (Davidson, 1986). Instead the curves decreased monotonically for both medium and small crabs. Thus during feeding, small mussels became the theoretically most profitable size. However, as with C.maenas, for a given size mussel, profitability levels were higher for larger crabs. The greater ability of C.novaezelandiae to open and consume large mussels more efficiently than portunids therefore explains differences in the shape and slope of the profitability curves.

Unlike mussels, C.maculosa profitability curves decreased monotonically with prey size for small and medium size C.novaezelandiae. Hence smaller whelks were more profitable than large whelks. This is because the rate of energetic intake was exceeded by the rate of handling time with increased prey size. Thus large whelks required greater time to break, open and

consume flesh and the energetic "worth" of the prey was reduced. Profitability curves for large crabs on the otherhand, remained constant regardless of whelk size. All whelks therefore were approximately similar in profitability.

Lawton and Hughes (1985) demonstrated similar monotonically decreasing profitability curves for small (55-65 mm carapace width) and medium (75-85 mm carapace width) Cancer pagurus when presented with L.littorea and N.lapillus. O.truncatus when presented with B.nanum and N.atramentosa showed generally decreasing profitability curves with increased prey size. Curves for medium and large crabs showed distinct peaks indicating optimum prey size. The absence of such peaks for C.novaezelandiae may be due to a lower efficiency of handling all size ranges of gastropods in comparison with portunid crabs.

Profitability curves for C.novaezelandiae feeding on M.edulis aoteanus, C.stutchburyi, C.maculosa and T.smaragdus showed significant differences in both the slope and height. Also the value of prey varied with prey size and crab size. As energetic value remains constant for a given prey size, the trends in profitability observed for C.novaezelandiae can be explained in terms of differences in handling time. At small prey size, despite cockles containing a lower energetic content than mussels, the time taken to open and consume cockles was much lower than that for the other prey species. Hence for small prey size, cockles had greatest prey value. However, for medium prey, the time required to handle mussels closely resembled that for

cockles and thus both species showed very similar prey value. At large prey size, however, the time taken to handle mussels increased at a slower rate than that for cockles. Thus, because handling times were lowest for mussels in comparison with the other three prey species, mussels become most profitable prey with increased prey size. Since handling times for bivalves were much shorter than gastropods, profitability of bivalves were generally greater in comparison with gastropods for small and large prey sizes.

Profitability curves are a useful tool when examining the theoretical aspects of crab feeding ecology as they enable the determination of optimum prey size and species. These curves therefore allow us to predict "a priori" what size or species of prey crabs should theoretically choose if given the choice. Once predictions have been tested, findings can therefore be applied to the Energy Maximization Premise.

Based on profitability curves derived for C.novaezelandiae in the present study, the following predictions can be made.

When given a choice :

1] All crabs should prefer large mussels over medium and small sizes.

2] Large crabs should prefer larger mussel sizes than medium and small crabs.

3] Medium and small crabs should prefer small whelks to larger whelks.

4] Large crabs should show no size preference for whelks.

5] Large crabs should prefer larger whelk sizes than medium and small crabs.

6] At small prey sizes (10-20 mm) cockles should be preferred over mussels by large crabs.

7] At medium prey sizes (28-35 mm) mussels and cockles should be chosen in equal proportions by large crabs.

8] At large prey sizes (40-45 mm) mussels should be preferred over cockles by large crabs.

These predictions were tested and will be discussed in the following section.

Prey-Size And Species Selection With Application To The Energy Maximization Premise.

Through natural selection, the foraging behaviour most beneficial to the fitness of the individual should evolve (Blundon and Kennedy, 1982). Theoretically therefore, animals should feed in a manner so as to maximize energy intake, yet minimize the potential of being eaten. The maximization of feeding efficiency has gained considerable attention, and to date, the Optimal Foraging Theory has become the most popular theory put forward. Many studies have examined and tested this theory (refer to earlier references); however, not all of the studies have confirmed the predictions. Even so, the presence of such a theory provides a useful foundation for rigorous testing

and refinement of our understanding of predator-prey dynamics.

Proponents of the Optimal Foraging Theory attempt to predict the behaviour of animals "while they are foraging" (Pyke, 1984). One component of this theory is the "Energy Maximization Premise" which has been applied in numerous brachyuran studies. The Energy Maximization Premise states that a predator chooses its diet to maximize the net energy intake per unit foraging time (Elner and Hughes, 1978). Therefore if given a choice of two prey sizes or species of differing value the predator should choose the one that maximizes energy intake.

Previous studies have demonstrated selection of optimal prey size for some brachyuran species. These studies have demonstrated that C.maenas (Elner and Hughes, 1978) and O.truncatus (Chilton and Bull, 1986) selected the optimal prey size when presented with a choice, and would choose progressively less valuable prey when optimal sizes were not available. The authors of both studies concluded that crabs were actively selecting prey size of greatest energetic value in order to maximize net energy intake. Crabs that exhibit such selection have been termed as "energy maximizers" (Hughes and Seed, 1981). However, Blundon and Kennedy (1982) suggest that selection of larger prey sizes was related to the greater opportunity of encountering prey with a greater surface area in comparison with smaller prey. This aspect of selection has yet to be fully examined.

Other studies have shown that many crab species do not select predicted optimal prey size. These species include L.puber (ap Rheinallt, 1986), O.catharus (Davidson, 1986), C.sapidus (Blundon and Kennedy, 1982) and C.pagurus (Lawton and Hughes, 1985). Instead of selecting greatest energetic prey size, crabs chose prey size that minimized time spent handling prey. These crabs have been described as "time minimizers". A possible reason why crabs minimize time spent foraging is to reduce vulnerability to predation by birds, fish and invertebrates. A reduction in time spent foraging in the open would be a distinct advantage, particularly to crabs that undertake regular excursions in the intertidal region.

In the present study, predictions made for C.novaezelandiae based on the Energy Maximization Premise were both confirmed and rejected depending upon prey size and species combination presented. C.novaezelandiae did not select the theoretically optimal mussel and whelk size classes as predicted by Prediction 1 and 3. Also large crabs did not randomly consume all whelk size classes as predicted by Prediction 4. Instead crabs preferred medium sized prey which were less economical than large mussels or small whelks. However, for crabs to feed optimally when presented with large mussel sizes of high energy content, required a considerable amount of handling time. Small whelks, although having a low energy content, required small handling times and thus their profitability was high. Yet large numbers of small whelks had to be consumed to obtain the same amount of energy contained in larger whelks. Therefore, crabs were able to

open medium size prey more quickly than large prey and therefore were able to feed on a greater number of prey. Thus a "trade off" existed in which C.novaezelandiae considerably increased its energetic intake by minimizing time spent opening and consuming a large number of prey items. Therefore if C.novaezelandiae is given a choice of prey size, it exhibits a time minimizing foraging behaviour.

Predictions 2 and 5 were confirmed by C.novaezelandiae with large crabs choosing larger prey sizes than medium and small crabs. Thus larger crabs did select prey of higher profitability. As a result, despite larger crabs consuming similar numbers of mussels and whelks in comparison with small and medium crabs, larger crabs exhibited a considerably higher energy intake. Selection of larger prey size with increased crab size was most likely related to greater crushing capabilities (and hence lower handling times) of larger crabs. This has also been observed for O.punctatus (Du Preez, 1984) and Panopeus herbstii (Seed, 1980). Furthermore, the selection of most profitable prey species as predicted by Predictions 6,7 and 8 were also confirmed. The preferential selection of prey species with highest energy value was due to crabs selecting prey species requiring least amount of handling time. With medium prey size, both cockles and mussels required similar handling times and hence crabs showed no species preference. Therefore for all three prey sizes, crabs selected species that maximized energy intake. Thus C.novaezelandiae switched its foraging behaviour to being an energy maximizer.

Similar findings have also been demonstrated for other crab species. C.pagurus preferred the gastropod L.littorea, a high profitability prey rather than N.lapillus when offered a choice (Lawton and Hughes, 1985). The authors suggested that such selection was based primarily on passive mechanical selection, as L.littorea was more easily handled due to a lower predatory resistance. L.rudis had a higher profitability value than L.nigrolineata of the same size due to a difference in handling time (Elner and Raffaelli, 1980). When both species were presented to C.maenas, L.rudis was preferentially chosen.

It is suggested here that C.novaezelandiae exhibits a flexible foraging strategy when feeding on bivalve and gastropod prey. The ability to switch from being a time minimizer to a energy maximizer permits a more adaptable and efficient foraging behaviour. When prey of different size or species are encountered, the flexible foraging behaviour of these crabs allows them to maximize the amount of energy return per unit foraging time. Such a behaviour would allow efficient utilization of prey encounters with both bivalve and gastropod species by simultaneously maximizing energy intake and minimizing time expenditure.

A similar flexible foraging behaviour has been demonstrated for O.catharus (Davidson, 1986). It has been suggested that acceptance or rejection of prey in response to prey contact and encounter rate, the reduction of handling times by learning, the vulnerability assessment of large prey, prey switching and the

discarding of unfinished mussels showed that O.catharus was able to modify its foraging behaviour as the need arose.

The evolution of such a flexible foraging behaviour probably arose in response to changing prey characteristics including distribution, density, size, vulnerability and availability of other prey, and predation pressures by birds and fish. It has been suggested that the development of a flexible behaviour permits crabs to feed optimally on patchily distributed prey, and where the prey population consists of similar sized individuals. It is expected, therefore, that a flexible foraging behaviour allows C.novaezelandiae to utilize mollusc prey which are typically patchily distributed within Lyttelton Harbour (Knight, 1971).

CHAPTER FIVE

GENERAL CONCLUSIONS AND SUMMARY

The New Zealand cancer crab Cancer novaezelandiae was shown to be a predator of a wide range of sessile and slow-moving benthic macro-invertebrates. Crabs collected from Lyttelton Harbour fed predominantly on molluscs, particularly bivalves, gastropods, and crustaceans. In the laboratory, crabs were shown to readily feed on four mollusc species of differing size and structure. When presented with various combinations of prey size and species crabs exhibited an efficient flexible foraging strategy. This strategy suggested that C.novaezelandiae was capable of maximizing energy intake per unit handling time.

The morphology of the feeding apparatus of C.novaezelandiae is designed to handle a diverse array of prey types. The large polyfunctional chelae are capable of exerting strong compressive forces, and together with large setose mouthparts, including stout mandibular processes and heavily calcified gastric mill ossicles, function together as very effective ingesting and crushing devices. The efficiency of this device is reflected in the diversity of food types encountered in the diet. The feeding apparatus has permitted C.novaezelandiae to specialize on molluscan prey which are abundant within the benthos of rocky shores and harbours. The ability of C.novaezelandiae to exploit this food resource is reflected by the absence of intraspecific differences in diet with respect to crab size, sex and season.

It is well documented that large, predatory crab species are important predators of molluscs (see Chapter Two). A number of these studies have demonstrated that changes in diet are correlated with crab size and seasonality. It has been suggested that changes in diet with crab size are a reflection of changes in the efficiency of the feeding apparatus, particularly with regard to the manipulative abilities and strength of the chelae. Moreover, seasonal changes in diet appear to be related to both the opportunistic behaviour of crabs and prey abundance. In the present study, however, for crabs greater than 40 mm carapace width no size or sexual differences in the feeding apparatus were obvious. The efficiency of the feeding apparatus appeared to remain constant with increased crab size (although compressive strength of the chela increases with crab size). All individuals have similar abilities to feed successfully on similar prey types. Also C.novaezelandiae appears to specialize on mollusc prey, despite the presence of other more accessible, easily consumed species, eg. coelenterates and Porifera. It is likely, however, that profitability of these species may be considerably lower than molluscan prey. It appears, therefore, C.novaezelandiae is primarily concerned with locating and consuming molluscs rather than opportunistically feeding on other food types encountered.

The ability of C.novaezelandiae to feed efficiently upon mollusc prey was demonstrated in the laboratory. C.novaezelandiae readily accepted four prey species of different geometric shape,

strength and profitability. The efficiency with which prey were consumed was influenced by many factors including crab size, prey size, shape and energetic value. Furthermore, C.novaezelandiae exhibited a flexible foraging strategy when given a range of prey individuals. When presented with a choice of bivalve or gastropod species of various sizes, C.novaezelandiae exhibited a time-minimizer foraging approach. However, when presented with a choice of two bivalve species of similar size, crabs switched to select prey species which maximized energy intake. Thus C.novaezelandiae feeds optimally under laboratory conditions. It might be expected therefore that a similar behaviour may occur under natural conditions, enabling them to maximize intake when feeding in either a dense or sparsely populated food patch.

In the laboratory, previous studies have shown that portunid crabs exhibited similar energy maximizing and time minimizing foraging approaches. However, the majority of these studies pertain to the availability of only one prey species. Few studies have investigated the influence of prey shape as a factor in prey selection. There is also a paucity of information regarding the influence of crab size, sex and breeding condition on the feeding ecology of brachyurans. These are serious oversights, particularly in the current dilemma of the applicability of Optimal Foraging Theory.

The Optimal Foraging Theory has recently been subjected to a good deal of scepticism with respect to its application to marine animals. The most critical view of the Optimal Foraging Theory is

that it is "tautalogical" (Ollason, 1970 cited in Pyke, 1984). Others suggest that the assumptions underlying this theory are implicit and should therefore be satisfied (or at least recognized) during experimental validation of the theory and associated components (Krebs, Stephens and Sutherland, 1983; Pierce and Ollason, 1987). Suggested criteria for evaluating studies that attempt to test this theory are given by Pyke (1984). Although such criticisms are admissible, it must be recognized that many of these assumptions are neither independent (and difficult to withhold) or measurable. Nevertheless, the Optimal Foraging Theory provides a useful tool for testing and subsequent remodification of hypotheses with respect to the dynamics of predator-prey systems.

Natural relationships between predator and prey are never static (Odum, 1971). Rather, both predator and prey are continuously evolving structural and behavioural adaptations in order to increase their survival chances (Krebs and Davies, 1982). Together these adaptations function to maintain co-existence between predator and prey such that no one species procures the upperhand (often referred to as the "arms-race; Dawkins and Krebs, 1979). Co-existence of predator and prey will depend on the extent to which different components of predation are stabilizing and destabilizing. With respect to brachyuran-mollusc relationships both have evolved adaptations in order to promote predatory and anti-predatory capabilities.

Throughout their evolution, molluscs have adopted a number of anti-predatory structures. The development of spines, increased shell thickness, and reduced spire height and aperture size in gastropods, and increase in size, shell thickness, degree of inflation and absence of a gape in bivalves have been suggested as responses to high brachyuran predation pressure (Boulding, 1984). Studies have demonstrated that in areas densely populated by crabs, gastropods are larger, and more robust in structure (Vermeij, 1976; Bertness and Cunningham, 1981). Populations of Nucella lapillus co-existing with large numbers of Carcinus maenas were more robust, with narrower apertures than in areas where these crabs were absent (Hughes and Elner, 1979). Fewer tropical clams have permanent gapes in tropical areas when compared with temperate areas and in shallow samples when compared with deep samples (Vermeij and Veil, 1978). It is postulated here that shell variation between closely related morphs are related to predation intensity. Once prey exceed the critical size of successful predation attack it obtains a size-refuge. Studies have shown that in areas of high brachyuran numbers, the prey population structure is dominated by small or large individuals, both above and below prey critical size (Boulding, 1984; Lawton and Hughes, 1985). Therefore, crabs play a very important biotic role in influencing mollusc distribution.

It has been postulated that anti-predatory adaptations of molluscs, although decreasing vulnerability, may not have evolved in direct response to crab predation (Stanley, 1975; cited in Boulding 1984). Instead the development of the mollusc shell

could be the result of morphological compromises in evolution, based on the trade off between reproduction, defence, feeding and locomotion. However, on the basis of this study, molluscs constituted a major proportion of the diet of C.novaezelandiae. This also appears to be true for many other large, predatory crab species. Therefore, development of any structural or behavioural features that lessen (even slightly) the vulnerability of mollusc prey to crab attack will be selected for. Thus the evolution of anti-predatory features of molluscs is therefore expected to be in direct response to brachyuran predation.

The development of molluscan anti-predatory structures most likely coincided with the development of crab features that promoted predator success. The evolutionary development of the Cancridae appears largely in response to feeding pressures. The development of the feeding apparatus of C.novaezelandiae appears to be well designed to feed efficiently on a wide variety of prey, particularly molluscs. From a paleontological perspective, the origin of brachyuran crabs capable of crushing and forcibly opening molluscs occurred in the Jurassic and earliest Cretaceous (Vermeij, 1976). Within these groups, the appearance of crabs capable of breaking large molluscan shells did not evolve until the Late Cretaceous and earliest Tertiary time. It is postulated by Vermeij (1975) that the increase in crushing capabilities of relatively small predators coincided with a decrease in the incidence of open-coiled and mechanically weak mollusc shells after the Cretaceous. This serves as a good illustration of the

impact of brachyuran predators on the morphology of mollusc species in the past.

The development of a flexible feeding strategy demonstrated in the present study appears well designed to maximize feeding in both limited and unlimited food situations. When faced with a sparsely or highly populated food patch C.novaezelandiae has the ability to switch behaviours so as to feed heavily on many, easily opened prey, or concentrate on larger, more time consuming prey. Both behaviours enable the crab to maximize energy intake. Furthermore, the ability to minimize time feeding serves to lessen the hazard of being eaten by fish and invertebrate predators. Remains of C.novaezelandiae have been observed in the guts of banded parrotfish (Pseudolabrus fucicola), blue moki (Latridopsis ciliaris), rig Mustelus lenticulatus) and octopus (Octopus maorum, pers. comm., C Duffy, 1988). Other anti-predatory devices of C.novaezelandiae include a sand-like, brown-red colour, and a general robustness of the carapace. Crabs capable of implementing a flexible foraging strategy would be expected to have a considerable advantage over more rigid feeders. This would enable the former to utilize a much wider range of feeding situations. The flexible foraging strategy of C.novaezelandiae may be one explanation why this species is widely distributed in many marine and estuarine habitats throughout New Zealand.

The feeding ecology of brachyurans is determined by many inter-related factors. Therefore investigations should examine

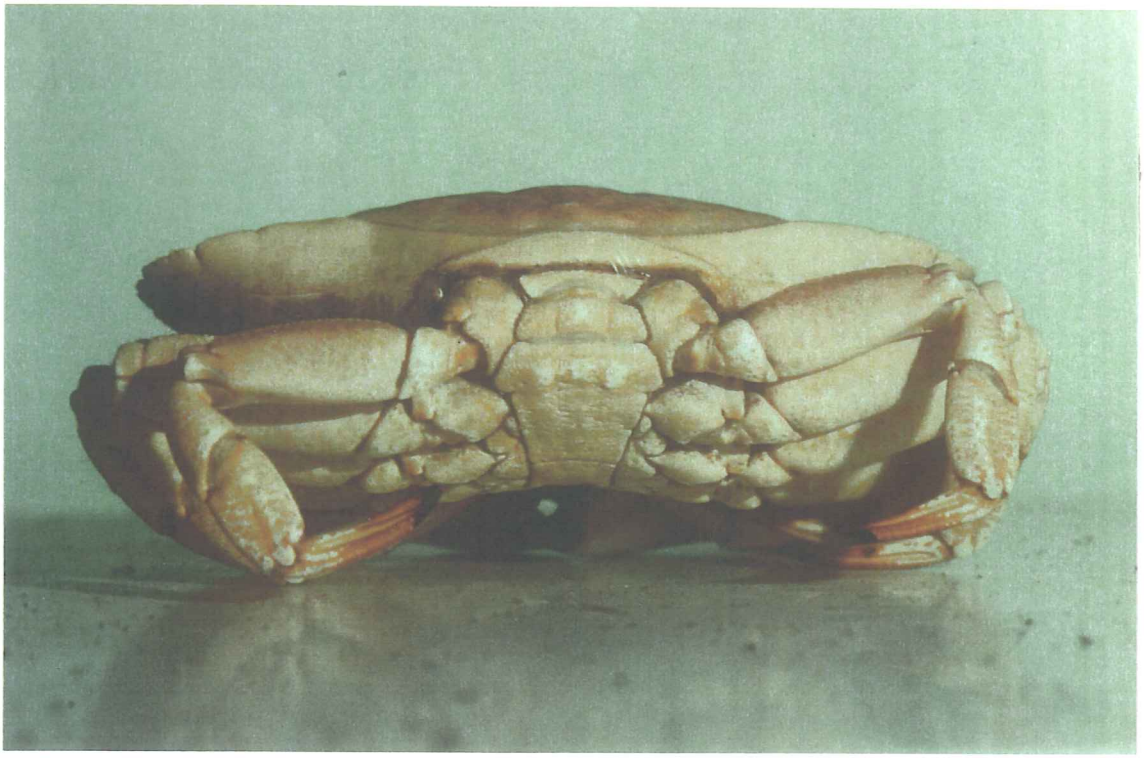
one behaviour when feeding on prey species of one particular size in the light of all other inter-related behaviours. Thus a framework approach must be adopted when examining brachyuran feeding ecology. Too few studies take this approach.

This study has investigated the feeding ecology of C.novaezelandiae and has shown the species to be a very efficient, well adapted predator of a variety of prey types, particularly molluscs. This species, therefore, is likely to exert strong pressures on other members of the harbour benthic community. Whether foraging by C.novaezelandiae affects natural prey population structure remains untested. However, Seed and Brown (1975; cited in Boulding, 1984) have shown certain sublittoral populations of Modiolus modiolus were deficient in size categories approximating the preferred size of Carcinus maenas and Cancer pagurus. Wear (1984) suggested that Ovalipes catharus may be responsible for the disappearance of toheroa Paphies ventricosa beds or instrumental in restricting post-settlement survival of this species to the upper shore and to high density refuge pockets. Diet studies by both Davidson (1987) and Wear and Haddon (1987) have subsequently found toheroa and other large bivalves are not an important dietary component of O.catharus. Davidson (1987) suggested that O.catharus is a predator of small burrowing bivalves, particularly during their stage of recruitment. Once bivalves reach a large size, they are capable of burrowing into the substrata, and thereby obtaining both a size and depth refuge. This has been experimentally demonstrated by Haddon, Wear and Packer (1987). Therefore because

O.catharus feeds predominantly on the early stages of bivalves, it may exert strong pressures on both bivalve recruitment and population structure. C.novaezelandiae is a predator of a wider range of molluscs species. Unlike O.catharus, it feeds on all later stages of molluscs and is capable of consuming a much wider size range. Therefore, bivalves would be required to reach a larger size in order to obtain a size refuge from C.novaezelandiae than O.catharus. Small bivalves may reach a refuge by burrowing into the substrate. It is not known how deep C.novaezelandiae is capable of locating and excavating infaunal molluscs.

Bivalve populations in harbours tend to be patchily distributed with high densities attracting predatory crab species (Knight, 1971). Such aggregations have been recorded for C.maenas (Walne and Dean, 1972), Panopeus herbstii (Whetstone and Eversole, 1978) and Menippe mercenaria (Menzel and Hopkins, 1958) where the authors estimated a consumption of 760,000 oysters per acre. Within the channels of Lyttelton Harbour there are extensive cockle beds and observations have shown that C.novaezelandiae tend to congregate within such areas. In addition to feeding on subtidal shellfish beds, cancer crabs migrate into the intertidal areas during periods of night time-high tides (Chatterton, pers. comm). Here they are exposed to a wider diversity of potential prey species including topshells, whelks, mussels and catseyes. This habitat which contains as many as eight co-dominant mollusc species is heterogeneous with respect to rocks, boulders and seaweeds (Knox,

1983). If predation occurs over a wide size range of individuals and many species, the effects of crab predation on the community may be less than in a assemblage dominated by a few species. C.novaezelandiae therefore has a flexible foraging behaviour which allows efficient feeding irrespective of population size, structure or heterogeneity. It is concluded here that C.novaezelandiae probably plays a very significant role in the benthic ecology of Lyttelton Harbour and its surrounding rocky shores.



THE END.

ACKNOWLEDGMENTS

I thank most sincerely my Supervisor, Dr Islay Marsden for her ever patient and dedicated support of this thesis. Her constructive criticism and advice were greatly appreciated.

Many thanks go to Dr Colin McLay for his assistance in identifying stomach contents, and for his useful criticisms and advice of this manuscript.

I would like to thank D. Tattle, G. Robinson, T. Carryer, B. Lingard and J. McKenzie for technical assistance. Thanks also to T. Robinson for her help and preparation of the manuscript.

I would like to express gratitude to my fellow colleagues. Especially Peter, Allen, Louise, Teri and Paul for their endless supply of parties, jokes, beers and their never-failing friendship and encouragement: Thanks Guys.

Finally, most special debt of gratitude must go to my parents for their support and never-ending encouragement to see this thesis through: Thank You.

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APPENDIX I

	MALES				FEMALES			
	Total Freq. of Occurr.	Percent Freq. of Occurr.	Total No. of Points	Percent Freq. of Points	Total Freq. of Occurr.	Percent Freq. of Occurr.	Total No. of Points	Percent Freq. of Points
Mollusca:								
Bivalves/Gastropods	57	39.0	2194.5	44.3	24	36.9	653.0	34.2
Cephalopods	2	1.4	140.0	2.8	1	1.5	40.0	2.1
Total	59	40.4	2334.5	47.1	25	38.4	693.0	36.3
Crustacea:								
Brachyurans	19	13.0	676.5	13.6	9	13.8	380.0	19.9
Shrimps	3	2.0	150.0	3.1	0	0.0	0.0	0.0
Amphipods/Isopods	14	9.6	340.5	6.9	9	13.8	261.0	13.7
Total	46	24.6	1166.0	23.6	18	27.6	641.0	33.6
Teleost	10	6.8	600.0	12.1	2	3.1	100.0	5.2
Porifera	2	1.4	58.0	1.2	0	0.0	0.0	0.0
Coelenterata	2	1.4	25.0	0.5	0	0.0	0.0	0.0
Algae	8	5.5	27.0	0.5	1	1.5	4.0	0.2
Unidentified Material	29	19.9	744.5	15.1	19	29.2	470.0	24.6
Total	146		4956.0		65		1908.0	

Appendix 1. C.novaezelandiae fore-gut contents from June 1985 to April 1987.

APPENDIX II

	SMALL (40 - 60 mm CW)		MEDIUM (61 - 100 mm CW)		LARGE (101 - 160 mm CW)	
	Total Freq. of Occurr.	Percent Freq. of Occurr.	Total Freq. of Occurr.	Percent Freq. of Occurr.	Total Freq. of Occurr.	Percent Freq. of Occurr.
Mollusca:						
Bivalves/Gastropods	3	30.0	48	32.9	30	52.6
Cephalopods	0	0.0	3	2.0	0	0.0
Total	3	30.0	51	34.9	30	52.6
Crustacea:						
Brachyurans	0	0.0	19	13.0	9	15.8
Shrimps	0	0.0	3	2.1	0	0.0
Amphipods/Isopods	4	40.0	15	10.2	4	7.0?
Total	4	40.0	38	25.3	13	22.8
Teleost	0	0.0	11	7.5	2	3.5
Porifera	0	0.0	2	1.4	0	0.0
Coelenterata	0	0.0	2	1.4	0	0.0
Algae	0	0.0	10	6.9	0	0.0
Unidentified Material	3	30.0	33	22.6	12	21.1
Total	17		146		90	

Appendix 2. C.novaezelandiae fore-gut contents of small, medium and large crabs from June 1985 to April 1987 (Sexes combined).

APPENDIX IIIa

	SPRING				SUMMER			
	Total Freq. of Occurr.	Percent Freq. of Occurr.	Total No. of Points	Percent Freq. of Points	Total Freq. of Occurr.	Percent Freq. of Occurr.	Total No. of Points	Percent Freq. of Points
Mollusca:								
Bivalves/Gastropods	10	27.8	339.5	27.5	14	32.6	462	33.0
Cephalopods	0	0.0	0.0	0.0	3	6.8	180	12.8
Total	10	27.8	339.5	27.5	17	39.4	642	45.8
Crustacea:								
Brachyurans	10	27.8	412.5	33.4	5	11.6	115	8.2
Shrimps	2	5.6	90.0	7.3	0	0.0	0	0.0
Amphipods/Isopods	1	2.8	90.0	7.3	3	6.9	60	4.2
Total	13	36.2	592.5	48.0	8	18.5	175	12.4
Teleost	3	8.3	170.0	13.4	4	9.3	300	21.4
Porifera	0	0.0	0.0	0.0	0	0.0	0	0.0
Coelenterata	1	2.8	5.0	0.4	0	0.0	0	0.0
Algae	1	2.8	2.0	0.2	2	4.6	7	0.5
Unidentified Material	8	22.2	215.0	17.4	12	27.9	227	19.8
Total	36		1236.0		43		1401	

Table 3a. C.novaezelandiae fore-gut contents on a seasonal basis for 1987.
(Sexes combined)

APPENDIX IIIb

	AUTUMN				WINTER			
Mollusca:								
Bivalves/Gastropods	23	32.6	866.0	48.7	34	40.9	1181.0	48.3
Cephalopods	0	0.0	0.0	0.0	0	0.0	0.0	0.0
Total	23	32.6	866.0	48.7	34	40.9	1181.0	48.3
Crustacea:								
Brachyurans	10	17.2	5.0	9.6	8	9.6	359.0	14.7
Shrimps	0	0.0	0.0	0.0	1	1.2	50.0	2.1
Amphipods/Isopods	6	10.3	132.0	11.9	13	15.6	329.5	13.4
Total	10	27.5	137.0	21.5	22	26.4	738.5	30.2
Teleost	3	5.2	140.0	7.9	3	3.6	90.0	3.7
Porifera	1	1.7	10.0	0.6	1	1.2	48.0	1.9
Coelenterata	0	0.0	0.0	0.0	1	1.2	20.0	0.8
Algae	1	1.7	6.0	0.3	6	7.2	16.0	0.7
Unidentified Material	13	22.4	375.5	21.1	16	19.2	354.0	14.5
Total	58		1777.0		83		2445.0	

Table 3b. C.novaezelandiae fore-gut contents on a seasonal basis for 1987. (Sexes combined).